Lion spatial socio-ecology: the effect of habitat on lion group dynamics.

by

Deborah Anne Donkin

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ABSTRACT

Lions are social, territorial animals that form prides of 2-18 individuals and hold territories ranging in size from 20 to 500 km^2. My aim was to investigate the effect of ecological processes on lion spatial demography, specifically to determine the effect of habitat structure, prey availability, and rainfall (predictability and variability) on lion group dynamics. I worked with an extensive database of lion observations (approximately 47000 over 29 years) from the Kruger National Park that had been recorded on monthly predator returns and in ranger diaries. I used the hypothesis of ideal free distribution to explain group dynamics across four physical habitat structures, namely, thickets, woodlands, mountainous areas and open tree savanna. There were larger groups of adults and more sightings than expected in the open tree savanna, while subadult and cub group sizes peaked in the woodlands. Using the resource dispersion hypothesis (RDH) as a base, I investigated lion group dynamics in relation to prey availability. I found agreement with the RDH, in that larger groups formed where their favoured prey species were in greatest abundance. Exclusively adult male and exclusively adult female group sizes increased with increasing buffalo abundance, while groups of adult males and adult females in mixed groups increased with increasing impala abundance. I used the mechanism of risk-sensitive foraging to explain the influence of rainfall on lion group dynamics. While group dynamics did not differ significantly across averaged mean annual rainfall regions or across seasons, it did differ between variability regions and between two years of extreme rainfall. The lions exhibited risk-prone behaviour across variability regions, forming larger groups in more variable environments. Finally, I combined the three factors to determine the relative importance of each in determining lion group dynamics across seasons. Wildebeest were important to adult female group dynamics, impala and buffalo to adult males, while buffalo abundance influenced functional group size. In the wet season, larger functional groups occurred in the areas of medium rainfall variability regardless of buffalo abundance. In the dry season, more groups of females than solitary females occurred in more variable environments with this trend reversed for males.

PREFACE

The experimental work described in this dissertation was carried out in the School of Life and Environmental Sciences (formerly the Department of Biology), University of Natal, Durban, from January 1998 to December 2000, under the supervision of Drs R.H. Slotow and M.G.L. Mills.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

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CHAPTER ONE
LION SPATIAL SOCIO-ECOLOGY: THE EFFECT OF HABITAT ON LION GROUP DYNAMICS

General Introduction

A population is defined by its demography and spatial ecology (Caughley 1977). The pattern of population distribution and abundance is determined by a number of environmental patterns and ecological processes. Environmental patterning refers to the spatial and temporal distribution of resources and abiotic conditions, while ecological processes include population growth, predator-prey interactions and foraging behaviour (Addicott, Aho, Antolin, Padilla, Richardson & Soluk 1987). Patterns and processes vary through space and time (Addicott *et al.* 1987; Menge & Olson 1990; Christensen 1997; Ostfeld, Pickett, Shachak & Likens 1997). The relative importance and interaction between these patterns and processes in shaping a community or population varies with spatial scale (Menge & Olson 1990; Levin 1992). While factors such as predation or humidity act on a local scale to influence local scale community ecology, larger spatial scales are associated with increases in the relative influence of variation in environmental conditions such as rainfall (Menge & Olson 1990).

The scale at which one works determines whether the environment studied is homogeneous or heterogeneous. A homogeneous environment is one in which patterns and processes do not change through space or time. A heterogeneous environment is one in which spatial and temporal patterns of physical and biotic factors vary (Ostfeld *et al.* 1997). These patterns may either be fixed or dynamic (Ostfeld *et al.* 1997). Heterogeneity is an important constituent in sustaining ecosystem function (Christensen 1997) and in the maintenance of species diversity (Rosenzweig 1995).

In a heterogeneous environment resource distribution and abundance may vary resulting in patches of good and poor quality habitat. Quality is a relative term, as a habitat that would be considered suitable for one species may not be preferred by another. The distribution of these patches through space will influence the distribution and abundance of animals. The way in which animals select a habitat has been the subject of much debate, with many theories using the process of foraging behaviour as an explanation. These theories base the animals' choice on food availability in terms of distribution, quality and quantity (e.g. Abrahams 1986, Mangel & Clark 1986, Gray & Kennedy 1994, Kohlmann & Risenhoover 1997).

These theories centre on the optimisation of foraging behaviour, predicting that animals should forage in such a way as to maximise their energy intake (Regelman 1984). The optimal foraging theory essentially states that foraging behaviour has been shaped by natural selection so that foraging strategies, which maximise fitness, will exist in nature. These foraging strategies will be optimal with respect to criteria that may be evaluated independently of knowledge of the animal's fitness (Pierce & Ollason 1987). Although fitness was initially defined and measured in terms of reproductive success and net reproductive performance (Williams 1966; Stephens & Krebs 1986; De Jong 1994; Ridley 1995), it is currently also referred to in terms of energy or food acquisition (Sih 1980; Krause 1994); the risk of predation and parasitism (Milinski & Heller 1978; Slotow & Rothstein 1995); access to mates (Krause 1994) and access to good-quality habitats (Barash 1977). The definition of fitness used by a researcher often depends on the question/ problem studied. Fitness definitions can be short-term or long-term, and measure either abundance or risk minimisation, and are either relative (extrinsic) or absolute (intrinsic) (Stearns 1986). The definition of fitness as it relates to resource acquisition is generally the definition that is used in terms of foraging theories and models such as the ideal free distribution theory (IFD) (Fretwell & Lucas 1970). In these cases, fitness is measured in terms of the animal's short-term rate of food or energy intake; the rate of intake must be optimised in order to maximise the animal's fitness.

Two basic models of optimal foraging include prey and patch models. While the question asked by prey models is whether a predator/ forager should search or eat, patch models ask for how long a forager should stay in a patch (Stephens & Krebs 1986). However, both models assume that individuals are optimising their energy intake. I have chosen to use ideal free distribution (patch model) and resource dispersion hypothesis (prey model) as mechanisms to explain animal distribution in a heterogeneous environment.

Habitat

How a population is distributed through a given area is influenced by the availability of suitable habitats (Pienaar 1974; Stander 1991; WallisDe Vries 1996; Perrin & Everett 1999). Although various habitats may be inhabited by a given species they are never of the same quality.

Fretwell & Lucas (1970) formulated the theory of ideal free distribution (IFD), an optimal foraging model that predicts the equilibrium distribution of organisms among patchy resources. IFD has the following assumptions: a) resources are distributed in patches. b) Intraspecific competitors are equal in all respects, i.e. they have the same ability to extract resources from the

environment and to compete with each other through interference and that they are "free" to settle in any patch. c) Individuals will settle in the patch with the highest intake rate at the time of their arrival. Travel time between patches is negligible thereby allowing individuals to move freely between the patches. d) Individuals have perfect knowledge of resource profitability (i.e. they are 'ideal'). e) Resource density remains constant through time: there is no depletion. f) Intake rate increases with resource density in a patch and decreases with number of competitors (Abrahams 1986; Kacelnik, Krebs & Bernstein 1992). In an area with two patches of different resource quality, one rich the other poor, the first individuals entering the area will settle in the resource rich habitat. As more individuals settle in this resource rich habitat, the availability of the resources decreases. A point is reached when it is more profitable for new individuals entering the area to settle in the habitat where, although the resources are in lower supply, the competition is less. Therefore, initially the fitness payoff will be greater in the resource-rich habitat but as more individuals settle in the area, the fitness payoff in both habitats will be similar. Individuals or competitors will adjust themselves according to the habitat quality so that each individual enjoys the same rate of resource acquisition (Krebs & Davies 1993). IFD predicts that the ratio of individuals to food will be equal and that the intake rate will be equal in both habitats.

In natural populations, the assumptions of IFD are often not met (Bernstein, Kacelnik & Krebs 1988). Food/ resources deplete over time, not all competitors have the same ability to acquire food and often movement between patches is not a viable option. Further complications are introduced in a predator-prey system where the food source is normally mobile and predators may be territorial thereby actively excluding competitors from a patch. These complications have led to modifications of the classical IFD as summarised by Kacelnik *et al.* (1992).

As an alternative to the classical IFD, Abrahams (1986) proposed the perception limitation model (PLM). This model works on the basis that there will be a point when animals will no longer be able to perceive the difference in resource availability between two habitats. The main assumption is that animals assess patch suitability from perceived intake rates rather than from the total amount of food available in that patch (Abrahams 1986). It predicts that any manipulation which increases the proportion of animals that must guess which patch to use, will increase deviation away from an IFD. It also predicts that intake rates should vary between patches, unlike IFD, where potential intake rate at equilibrium is equal for all competitors regardless of patch quality.

While both IFD and PLM may be used to test animal distribution in an area, food is not the only resource determining animal distribution. Other resources including mate availability during the breeding season (Gittleman 1989), presence of suitable nesting/ den sites (Báldi & Csörgő 1994), and the availability of surface water also play a role in an animal's habitat selection (Pienaar 1974; Hunter 1996). However, resource availability is not the only factor influencing a population's spatial distribution. It is also affected by the distribution of interspecific competitors (Sinclair 1985) and by the relationship between conspecifics themselves (McComb, Packer & Pusey 1994).

In this project, I have divided one reserve (Kruger National Park) into four habitat/ landscape types (open tree savannah, mountainous areas, woodlands and thickets) based on the physical structure of the vegetation (degree of openness) and basic topography of the area. The four habitats do not have equal coverage throughout the park. They offer different advantages and disadvantages to lions (*Panthera leo*) that settle in the area, such as amount of cover for hunting and hiding places for cubs from infanticidal males. Based on IFD, I predicted that there would be larger groups and more sightings of lions in more favourable/ good quality habitats while smaller groups and fewer sightings will characterise poor quality habitats. This is developed further in Chapter Two.

Sociality and predator-prey relationships

Many animals lead a solitary existence, only coming together for brief periods during the mating season or when raising young (Kitchener 1991). These animals may live in relatively close proximity to one another but the majority of their daily activities, such as foraging, are carried out alone. The area or resources used by a solitary animal may form part of a territory that they either actively defend or that overlaps with those of conspecifics without the occurrence of aggressive encounters (Kitchener 1991). However, many animals are social, occurring in groups of varying sizes and varied degrees of relatedness (Ross, Vargo & Keller 1996). These animals may co-operate in activities such as foraging/ hunting (Kleiman & Eisenberg 1973; Avilés 1993), defence of territory (Packer, Scheel & Pusey 1990) and care of young (Sherman, Jarvis & Braude 1992). While there are some disadvantages to group living, e.g. competing for food (Delestrade 1999) or mates (Henschel, Lubin & Schneider 1995) and greater conspicuousness to predators (Wright 1998), there are also advantages such as increased vigilance for predators (Van Schaik, van Noordwijk, Warsono & Sutriono 1983; Hunter & Skinner 1998), the potential for social learning (Adler & Gordon 1992; Carlier & Lefebvre 1996) and the ability of predators to catch larger prey (Creel & Creel 1995). These advantages

are often species-specific and are related to unique patterns of social organisation (Barash 1977; Macdonald 1983).

When animals occur in groups, the possibility of successfully defending an area or territory increases (McComb *et al.* 1994). However, the size of the group, as well as that of the territory, is influenced by the resources in the area (Creel & Macdonald 1995; Meia & Weber 1996). The resource dispersion hypothesis (RDH) states that group size is determined by the quality or richness of the resource patches in the area while territory size is determined by the distribution of the resource patches (Macdonald 1983; Meia & Weber 1996). RDH predicts that larger groups will form in resource-rich areas and that territory size will be greatest when good quality patches are widely dispersed.

The size of a territory may be determined by the distribution of resources during "bad" seasons/ years when the animals have to cover a large area in order to obtain enough food (Macdonald 1983). However, during "good" seasons/ years, the animals' territory may be large enough to support additional group members (Hersteinsson & Macdonald 1982). During these times, the relationship between individuals may be the factor determining whether new members are accepted into a group. It may merely be a case of juveniles or subadults remaining with their natal group instead of dispersing (Macdonald 1983; Blackwell & Bacon 1993) or, the non-aggressive acceptance of a new individual in the territory (Macdonald 1983; Meia & Weber 1996). Lions maintain territories that vary very little in size over time regardless of pride size (Bertram 1973). They will however, recruit new members into the pride from the female subadults that are born into the pride. The adult males evict all males born into a pride once they reach about four years of age (Hanby & Bygott 1987).

In terms of social predators, group size may be correlated with prey density (Creel & Macdonald 1995), smaller predator groups occurring where their prey is least abundant and, larger groups occurring where prey is in great abundance. However, there are also other behavioural and biological factors that will affect the group size of social predators such as relatedness between individuals, territory defence and defence of young. In Chapter Three, I investigate how prey distribution and abundance affect lion distribution and group size, predicting that larger groups of lions will be found in resource rich areas, where resource refers to prey availability, while smaller groups will be found in areas of low prey availability (resource poor areas). The distribution of the lions should be positively correlated with that of

their preferred prey species if it is this factor that has a controlling influence over lion distribution.

Rainfall

Rainfall affects animal population dynamics, although this is generally an indirect effect rather than a direct influence on the population (e.g. Bergallo & Magnusson 1999). As rainfall affects habitat structure (Bronikowski & Webb 1996; De Bie, Ketner, Paasse & Geerling 1998), it may affect an animal's habitat preference (Heinsohn & Heinsohn 1999; Van Heezik & Seddon 1999) and diet (Roberts & Dunbar 1991). It also affects reproduction in seasonal breeders (Taylor & Green 1976; Underwood 1982), although there is very often a time lag associated with the population's response (Fichet-Calvet, Jomâa, Ben Ismail & Ashford 1999).

Rainfall as a process can be viewed in terms of its predictability and variability. However, as few species are directly correlated with rainfall, one cannot use rainfall to accurately predict population dynamics (Swanson 1998). Variability in rainfall through space and time results in a heterogeneous environment in which environment quality or resource availability will vary. Variability in resource availability and its effect on foraging behaviour has been well documented in birds (Caraco, Martindale & Whittam 1980; Caraco 1981a & b, 1982, 1983; Tuttle, Wulfson & Caraco 1990). The reaction of an animal to variability in resources is described in terms of risk-sensitive foraging (Stephens & Krebs 1986). An animal or group may react in a risk-prone or risk-averse manner. If a forager was presented with two resource options, one constant and predictable, the other variable (sometimes no reward, sometimes reward greater than constant reward), a risk-prone forager will select the variable resource while the risk-averse forager will choose the predictable, constant reward.

In terms of predators, rainfall has an indirect effect on predator distribution and group dynamics through its effect on the distribution of their prey species (East 1984; Stander, Haden, Kaqece & Ghau 1997). Herbivores may form larger groups during the wet season when resources are abundant while groups may break up during the dry season when resources are scarce resulting in the formation of small predator groups in the wet season and larger predator groups in the dry season. However, in areas where a constant water supply is available through the provision of waterholes, during the dry season, when surface water is unavailable, many herbivores are restricted to the areas around waterholes (Ritter & Bednekoff 1995). This may result in a concentration of predators at the waterholes. During the wet season, when there is surface water available, the prey may be more dispersed resulting in a wider distribution of predators. Predator

group size may therefore be greatest in the wet season when prey are more dispersed (food supply is more variable through space) and smaller in the dry season. The animals would be exhibiting risk-prone behaviour in the dry season as they are forming larger groups when their prey resource is more variable. However, larger groups have increased hunting success and can hunt larger animals (Kruuk 1972; Cooper 1990), thereby enabling all individuals in the group to fulfil their daily minimum energy requirements. In an environment with no constant water supply, social predator group size may increase during the dry season when prey are scarce and decrease during the wet season when prey are in abundance, resulting in larger predator group formation and thus risk-prone foraging in the dry season.

Scale

Environmental patterns and ecological processes vary through space and time resulting in heterogeneous environments (Addicott *et al.*1987; Menge & Olson 1990; Christensen 1997). Long-term studies are therefore vital if one is to determine how slow processes and, process interactions, influence populations through time, especially for higher plants and animals (Franklin 1989). The spatial scale of a project is also crucial in determining the relative importance of variables such as habitat quality and resource dispersion on population dynamics.

My project focuses on the influence of three factors on lion spatial socio-ecology, namely structural habitat selection, prey availability (resource distribution and abundance) and rainfall. I have obtained an extensive historical database of lion sighting information from the Kruger National Park (KNP) dating from 1957 to 1985. This provides a unique opportunity to investigate the influence of broad-scale patterns and processes on lion dynamics within one reserve using a database that not only has a large temporal scale (29 years) but where there is also a large spatial scale (KNP area = 19 500km^2).

Lions have been widely studied in southern and east Africa. Aspects of, and reasons for their sociality as well as their habitat and prey choice have been studied in a number of areas and over many years (e.g. general - Schaller 1972; population studies - Bertram 1973; Smuts 1976; Stander 1991; Mills, Biggs & Whyte 1995; Creel & Creel 1997; co-operation/ sociality – Caraco & Wolf 1975; Packer & Pusey 1982; Van Orsdol, Hanby & Bygott 1985; Packer & Ruttan 1988; Packer *et al.* 1990; Scheel & Packer 1991; Pusey & Packer 1994; Grinnell, Packer & Pusey 1995; predation/ foraging – Rudnai 1974; Van Orsdol 1984; Ruggiero 1991; Mills & Shenk 1992; Stander 1992a & b; Funston, Mills, Biggs & Richardson 1998; subadult emigration – Hanby & Bygott 1987). However, none of these studies, with the exception of the Serengeti

lion project, which was initiated in 1966 (Packer & Pusey 1997) and a study by Mills *et al.* (1995; 24 years of data used) have been carried out using data from extended periods of time. Although significant studies have been carried out in the fields of group dynamics, predator-prey interactions or ecological influences, some have been carried out over short time periods, using small numbers of prides and over a small area (Table 1.1). My project thus has the advantage of data collected over a long time scale (29 years) in a uniform manner (monthly predator returns); as well as the fact that comparisons between lion group characteristics are made between structural habitat types within one large reserve (19 500km^2).

Table 1.1. Lion studies where group dynamics, predator-prey interactions and ecological influences on group dynamics have been carried out. The temporal and spatial scales over which some of these studies were done have been of short duration or over a small area with limited number of lions.

=	Reserve	Area (km^2)	Habitats[a]	Number of prides	Study duration (years)	Source
1	Central district & Crocodile Bridge area of Kruger National Park, South Africa	6023	5	63	2	Smuts (1976)
2	SE of Kruger National Park	235	1	5	4	Mills & Shenk (1992)
3	Central district of Kruger National Park	5500	4	+/- 60	24	Mills *et al.* (1995)
4	Etosha National Park, Namibia	22270	3	12	4	Stander (1991)
5	Hluhluwe-Umfolozi Park, South Africa	960	3?	114 lions	11	Anderson (1980)
6	Hluhluwe-Umfolozi Park	+/-480	unspecified	6	0.5	Maddock *et al.* (1996)
7	Manovo-Gounda-St.Floris National Park, Central African Republic	330	2	3	5	Ruggiero (1991)
8	Nairobi National Park, Kenya	115	5	25-35 lions	4	Rudnai (1974)
9	Queen Elizabeth National Park, Uganda	150	2	3	2.42	Van Orsdol (1984)
10	Rwenzori National Park, Uganda.	150	2	3	2.67	Van Orsdol (1982)
11	Selous Game Reserve, Tanzania	2600	6	3+	2.83	Creel & Creel (1997)
12	Serengeti National Park, Tanzania	Seronera	1	2	7	Bertram (1973)
13	Serengeti National Park	Seronera	1	2	7	Bertram (1975)
14	Serengeti National Park	2250	2	20	14	Pusey & Packer (1987)
15	Serengeti National Park	2250	3	15-20	+/- 24 years	Packer *et al.* (1988)
16	Serengeti National Park	unspecified		21	3.42	Packer *et al.* (1990)
17	Serengeti National Park	1950	2	13	28	Hanby, Bygott & Packer (1995)
18	Seven reserves including Kalahari Gemsbok N.P., Kruger N.P., Lake Manyara N.P., Nairobi N.P., Ngorongoro Crater, Queen Elizabeth N.P., Serengeti N.P.		10	125	taken from 13 studies of lions ranging between one and four years duration	Van Orsdol *et al.* (1985)

[a] Habitats refers to areas of different habitat structure and/ or prey composition
Note: N.P. refers to National Park.

Lions

Lions are the only true social felids (Kleiman & Eisenberg 1973), with two to 24 individuals associating to form prides (Stander 1991; Funston & Mills 1997; Whitman & Packer 1997; Yamazaki & Bwalya 1999). A pride consists of several females together with their offspring (subadults and cubs) which may be joined by a group of males (coalition). Lions are territorial, their pride ranges may vary between 20km^2 and 650km^2 in size (Smuts 1976; Stander 1991; Funston & Mills 1997). The area is usually fixed, although it may vary slowly with time (Bertram 1973; Pusey & Packer 1987), and is determined by the availability of food, water and the presence of other prides (Orford 1986; Stander 1991).

Prides are fission-fusion groups that may split into several subgroups or semi-permanent subprides scattered throughout the pride area/range (Schaller 1972; Packer *et al.* 1990). The subgroups vary in size, but the same individuals associate consistently (Schaller 1972). Females also spend a considerable amount of time alone (Pusey & Packer 1987). The grouping pattern of females results from a variety of factors such as cub defence and the maintenance of a long-term territory (Packer *et al.* 1990; Pusey & Packer 1994).

Males form coalitions that compete for access to females (Pusey & Packer 1987). Larger coalitions can generally gain and hold tenure for longer than singletons or pairs of males (Bygott, Bertram & Hanby 1979). When males take over a pride, they evict all adult males and subadults. They also kill virtually all small cubs present in the pride (Pusey & Packer 1994). Males tend to hold tenure for periods of approximately two years before they are either ousted from the pride by stronger males or leave voluntarily (Bertram 1973; Pusey & Packer 1987). Therefore, it is essential that the males inseminate the females soon after they take over the pride in order to ensure the survival of their cubs (Pusey & Packer 1994). Females only come into oestrous 18 months after the birth of their cubs. However, if the cubs die the females resume mating within days or weeks (Packer & Pusey 1983).

Subadults are lions of two to four years of age. They are capable of hunting from the age of two years old (Packer *et al.* 1990; Scheel & Packer 1991). While female subadults often remain with the pride upon maturation, the males are always evicted (Bertram 1973). Where males and females do disperse, the males will disperse further than females (Pusey & Packer 1987).

Cub litter size in lions varies between one and four cubs, with the majority of litters consisting of two to three cubs (Packer & Pusey 1995). Although cub litter size does not appear to be influenced by food, cub survival is (Packer & Pusey 1995).

Lions & Habitat

Pride size varies from one area/habitat type to another and may also vary within an area/ habitat over time (Van Orsdol *et al.* 1985; Stander 1997). Van Orsdol *et al.* (1985) compared lion densities in ten different habitat types, focussing on the relationship between range/territory size and prey. Their results showed that range size was inversely correlated with prey abundance during the period of least abundance and that pride size and cub survival was strongly correlated with the lean season food abundance. The abundance of prey in a habitat will be limited by the availability of cover, food and water (Berry 1981; Ritter & Bednekoff 1995; Hunter 1996). Van Orsdol *et al.* (1985) also found that the physical features of the habitat influence the level of male-male competition and thus, indirectly the sex ratio within prides.

The structure of a habitat is important in determining how lions utilise an area. It has been found to have a significant effect on hunting success, i.e. the amount of cover supplied to the hunting lion is important (Van Orsdol 1984). Habitat structure also determines the prey species available in the area, as certain species prefer more open areas for grazing (e.g. wildebeest, *Connochaetes taurinus*) while others prefer more wooded areas for browse (e.g. kudu, *Tragelaphus strepsiceros*).

Lions & Prey

Lion group size varies with the abundance of prey, increasing when prey are scarce in order to increase the probability of attaining daily food requirements (Stander 1992a). When prey are abundant, lionesses in all group sizes including solitary foragers can fulfil/ exceed their daily minimum requirements (Packer *et al.* 1990; Stander 1992a). Smuts, Hanks & Whyte (1978) observed that the lions in central KNP produced cubs during the period when their major prey species produced their young. Nutrition has the greatest effect on cub survival therefore it is important that there is a high density of prey available (Van Orsdol *et al.* 1985). Prey distribution and vulnerability is therefore of importance to the maternal females (Sunquist & Sunquist 1989).

Lions prey on a number of species including buffalo (*Syncerus caffer*), wildebeest, zebra (*Equus burchelli*), impala (*Aepyceros melampus*), kudu, giraffe (*Giraffa camelopardalis*), warthog

(*Phacochoerus aethiopicus*) and waterbuck (*Kobus ellipsiprymnus*)(Bourliere 1965; Rudnai 1974; Van Orsdol 1984; Sinclair 1985; Ruggiero 1991; Mills *et al.* 1995). The presence or abundance of their preferred species will therefore influence lion distribution and density. The distribution of prey has been found to influence the distribution of male lions in the southern section of the Kruger Park. Funston *et al.* (1998) found that male lions in the southern section of the Kruger Park preferred the open tree savannah where their territories almost totally overlapped with those of the buffalo herds.

Lions & Rainfall

Rainfall might also be an important factor affecting lion population dynamics. Through its influence on habitat structure and thus available cover for hunting, rainfall may affect hunting success. As stated above, Van Orsdol *et al.* (1985) found hunting success improved with increased cover. Funston, Mills & Biggs (in press) found that while shrub cover did not have a significant effect on hunting success, hunting success increased significantly with grass height. Not only does rainfall have a direct influence on the habitat structure through its effect on the vegetation, but indirectly, through this influence on vegetation and general water availability, it will influence the distribution and condition of herbivores and hence the carnivores that prey upon them.

Mills *et al.* (1995) showed that herbivore populations react differently to the 10-year wet/dry rainfall cycles experienced in KNP and as a result differ in their vulnerability to predation. They found that wildebeest and zebra are more vulnerable to predation by lions during the wet cycle, while buffalo and waterbuck are more vulnerable in the dry cycle. They also indicated that buffalo were more heavily influenced by lion predation during periods of population decline than were wildebeest and zebra.

Kruger National Park

The Sabie Game reserve, (as the Kruger National Park was first known) which extended between the Sabi and Crocodile rivers, was proclaimed on March 26, 1898 (Stevenson-Hamilton 1974; Meiring 1982). Initially, the park faced much opposition as people saw it as their natural right to hunt the game. There was also opposition from the farmers, especially about the lions, which they regarded as vermin that should be shot (Stevenson-Hamilton 1974, Smuts 1982). Over the years, as the park was expanded, although there was still opposition to the idea of a protected reserve for wildlife, there was also growing support. As people learnt

more about the wildlife and once the reserve was opened for tourism, their hateful opinion of lions changed (Stevenson-Hamilton 1974).

At present the Kruger National Park (KNP) encompasses 19 485km^2 plus a further 2 000km^2 covered by private reserves which adjoin KNP and are managed as an integral unit. It extends between the Limpopo River in the north and the Crocodile River in the south, from the Lebombo Mountains in the east to a man-made border in the west (Fig. 1.1). The park has a fairly uniform topography sloping gradually west down towards the Lebombo Mountains. Altitude varies between 180 to 800 metres above sea level. Six main rivers drain the park (Fig. 1.1). There are also a number of seasonal rivers that only flow when it rains but they can retain water in pools for considerable periods.

There are also a number of boreholes across KNP, which allow for the provision of water to both game and people throughout the year. The boreholes were established as part of a water stabilisation program to overcome problems that may arise during long periods of drought (Pienaar 1985). The basis lay in the fact that the water distribution (both natural and artificial) in KNP was considered to be well below that which existed when the Sabi and Shingwedzi game reserves were first proclaimed at the turn of the century (Pienaar 1985). The prevention of migration of certain species out of KNP through the erection of fences was also an influential factor. During periods of natural disasters, animals that would normally migrate out of the areas could no longer do so. Therefore the permanent watering points were established as part of an effort to overcome the population crashes that could arise due to natural catastrophes. The first attempts at establishing artificial watering points for animals began as far back as 1929 and continued through a number of phases including the establishment of concrete dams and the placement of weirs in major river systems (Pienaar 1985). Today, the majority of the waterholes are within 10 km of each other, greatly reducing the need for species migrations through the park.

However, problems have arisen with the establishment of permanent waterholes throughout the park (e.g. Harrington, Owen-Smith, Viljoen, Biggs, Mason, & Funston 1999). The establishment of waterholes in northern KNP resulted in the movement of wildebeest and zebra into the area (Harrington *et al.* 1999). Zebra and wildebeest are major prey species of lions (Bourliere 1965; Rudnai 1974; Van Orsdol 1984; Sinclair 1985; Ruggiero 1991; Mills *et al.* 1995). There was thus an increase in the number of lions in the area, which then also preyed on the more rare roan antelope (*Hippotragus equinus*)(Harrington *et al.* 1999). The subsequent

closure of the waterholes in a section of the roan range resulted in the recovery of the roan herds (Harrington *et al.* 1999).

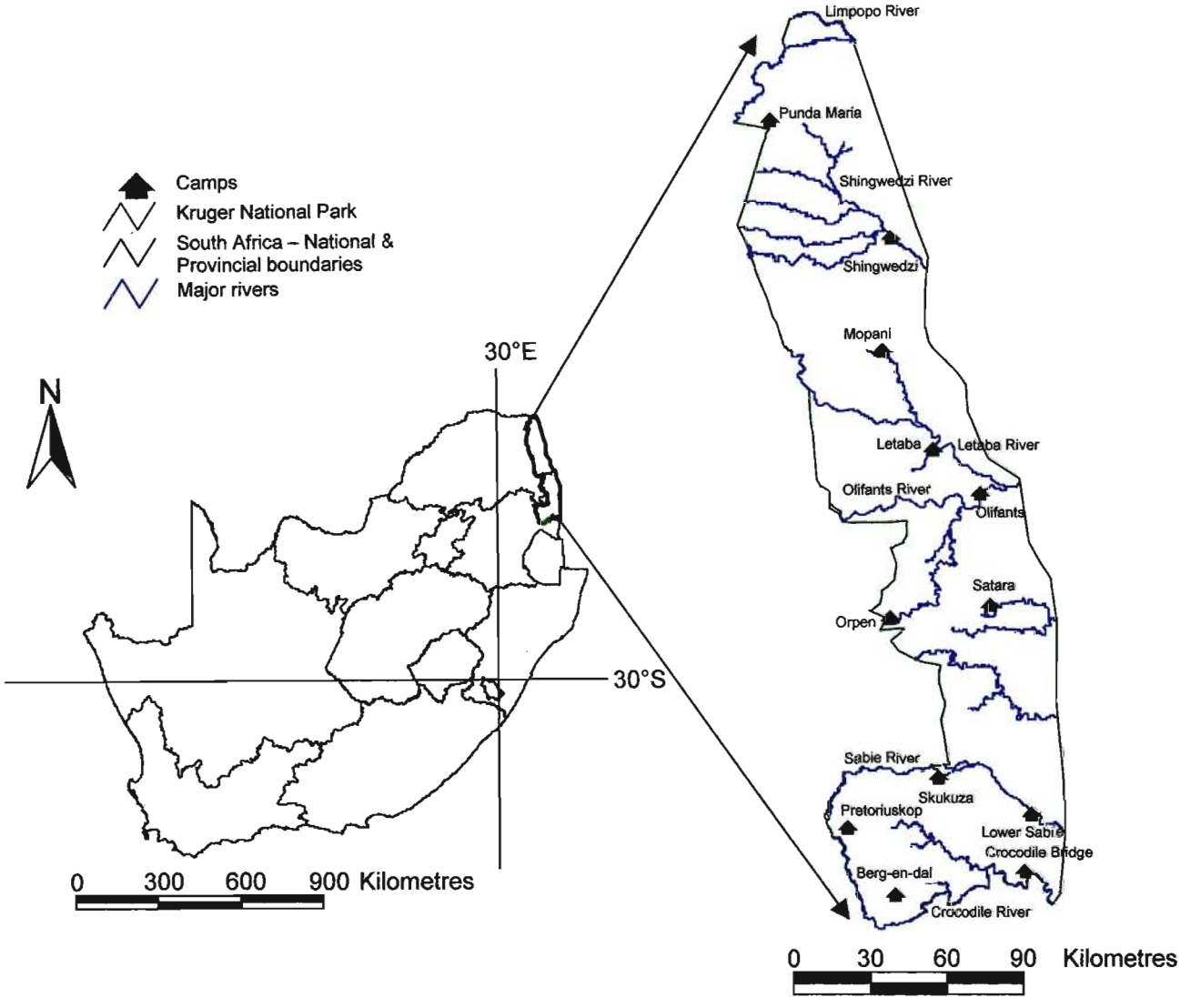

Figure 1.1. The Kruger National Park is situated along the eastern border of South Africa where it covers an area of 19 485km^2. There are six main rivers that drain the park.

The park was divided into 35 landscape types by Gertenbach (1983), who defines a landscape as an area with a specific geomorphology, climate, soil and vegetation pattern together with associated fauna. I divided KNP into four broad habitat types, namely the Marula plains on basalt in the east, the *Combretum* woodlands in the north-west, the *Acacia* thickets combined with the sour bushveld in the south-west, and mountainous areas, which include the Lebombo mountains and the Malelane mountain bushveld. Details of this are presented in Chapter Two.

The Kruger National Park is a summer rainfall region where wet and dry cycles follow each other at approximately 10-year intervals (Gertenbach 1980; Mason 1990). Periods of above and below the long-term average rainfall occur at regular intervals within the wet and dry cycles (Gertenbach 1980). The precipitation in KNP decreases from south to north, except for the area around Punda Maria, which is situated at a higher altitude. There is a minor decrease in rainfall from west to east that corresponds to the decrease in altitude. This becomes more pronounced towards the escarpment on the western boundary (Gertenbach 1980). Herbivore populations are influenced by the rainfall cycles. Most populations, except wildebeest and zebra, tend to decrease during dry cycles (Mills *et al.* 1995); while decreases in zebra and wildebeest populations, and increases in buffalo and waterbuck populations, have been recorded in the wet cycles (Gertenbach 1980; Mills *et al.* 1995). Initially lions were blamed for major decreases in certain prey species populations but it soon became evident that it was the effect of the high rainfall and long grass that played an important role in suppressing these animal populations (Whyte 1985). I look at the influence of prey abundance and distribution and the effect of variability in rainfall on lion group dynamics in Chapters Three and Four, respectively.

Aims & Objectives

Although studies have been done relating lion biology to prey biomass and rainfall (Van Orsdol *et al.* 1985; Mills *et al.* 1995), none have analysed lion demography in terms of the effect of variability in rainfall. Neither have comparisons been made between lion group characteristics within one reserve containing numerous habitat types. My study therefore undertakes to compare lion demography within one large reserve, the Kruger National Park, which consists of several different habitat types. The KNP provides an excellent opportunity to study a lion population in an area where there is little climatic variation but where there is variation in habitat structure, prey distribution/ abundance and rainfall. The KNP also has a large database of lion sightings dating from the late 1950s until 1985 which gives the added advantage of a large time scale to the study.

The specific aim of my project was to understand the ecological processes shaping lion spatial demography. The following chapters examine three factors, namely habitat structure (Chapter Two), prey distribution (Chapter Three), rainfall (Chapter Four) and how the combination thereof (Chapter Five) influence lion group dynamics. Final summaries and conclusions are discussed in Chapter Six.

In Chapter Two, I look at the effects of structural habitat on lion group dynamics. Specifically, my objectives were firstly, to describe the effect of physical habitat structure on lion group sizes and compositions and, secondly to determine in which habitat the lions have the highest reproductive output. The effect of prey abundance and distribution on lion group dynamics and prey selection is investigated in Chapter Three. My objectives were firstly to determine the influence of total prey abundance (prey base biomass) and that of specific individual prey species on lion group dynamics. Secondly, to describe the pattern of prey selection by lions in KNP and how specific prey availability, relative to the total prey base, influences lion group dynamics. In Chapter Four, I establish the effect of rainfall on lion group dynamics. As rainfall influences prey species' movement patterns and distribution through its effect on vegetation quantity and quality, so it should have an indirect effect on lion distribution. My objectives were to determine if lion group dynamics vary across actual rainfall regions and across seasons. I used two measures of region, firstly, mean annual rainfall regions and secondly, rainfall variability regions. In Chapter Five, I combine the significant factors from the previous chapters in order to determine their relative importance and combined influences on lion group dynamics.

General Methods

The methods used for map creation involved three Geographic Information System (GIS) programs, IDRISI for Windows version 2.0, Cartalinx version 2.0 and Arcview version 3.1. I refer to two types of files namely raster or grid images and vector files. A raster image is made up of small, internally uniform cells (pixels) arranged in a grid (Eastman 1997). A vector file stores a set of points (each referenced by a pair of locational co-ordinates) that describe either the locations of the features (if they are points), or their course/ boundary by means of a sequence of points that should be joined by arcs. There are three types of vector files: point, line and polygon (Eastman 1997).

The maps created for this project were based on an Idrisi raster image of the KNP obtained from Scientific Services, KNP. I chose a convenient working grid cell size of one minute^2 (1.6km * 1.8km) which gives a total of 15 444 cells. As I was working with broad scale patterns, this grid cell size allows for the detection of patterns in lion density and prey abundance across structural habitats while still providing for vegetation changes on a relatively small scale. There may have been areas which were not accessible to the rangers, therefore using a larger grid cell size, e.g. 10km^2, would have led to extrapolations from the data which are not necessarily true. Using as small a grid cell size as possible/feasible increases the accuracy of/confidence in the results obtained from the analysis. It also maximises the sample size of cells used in the analysis and maximises the variation of the habitat characteristics across the cells (Porter & Church 1987).

Lion sightings

Since its inception the KNP has been divided into sections, each maintained by a section ranger and accompanying field rangers. The section rangers manage the section, which involves, amongst other activities, patrolling by vehicle and at times on foot. Until the early 1980s, the field rangers were based at pickets in the section from which they did foot patrols into the surrounding area including patrols along the park boundaries. The field rangers are now housed in a central area at the section ranger's house.

Starting in the late 1950s, the number, age and sex of the lions seen by field rangers and section rangers were recorded on forms known as Monthly Predator Returns. These forms included columns for the date, location, grid reference, number of adults (males and females), subadults, cubs and comments (Appendix 1.1). The section rangers stationed throughout the KNP also kept diaries in which the activities of the day were recorded. These entries include lion sightings that in some cases were not recorded on the returns and/ or often offered a more detailed account of

the sightings. Bias is introduced by using the diaries, as not all rangers would have recorded every sighting they made of lions or entered the same amount of detail. The sections also differ in area, which may result in the roads in smaller sections being patrolled more often than those roads in larger sections. A further bias is added as the boundaries/ KNP borders are inspected more often than areas within the park.

A total of 59 757 lion sightings were captured from the monthly predator returns (January 1957 – September 1985) and diaries (April 1960 – December 1985) from 23 ranger sections throughout the Kruger National Park (Table 1.2). There are currently 22 sections in operation, which were established at different times, many of the larger original stations having been divided up into smaller sections.

Table 1.2. Lion sighting data captured from the monthly predator returns and diaries of 23 stations throughout the KNP. The number of entries varies between stations as the stations were established at different times and also covered different sized areas.

Station	Number of data lines captured	Date established
Houtboschrand	494	1982
Kingfisherspruit	6641	1955
Klipkoppies	1500	1964 - 1973 – became part of Mooiplaas
Krokodilbrug	2687	1902
Letaba	4145	1921
Lower Sabie	655	1977
Mahlangene	2211	1973
Malelane	6425	1919
Mooiplaas	617	1973
Nwanedzi	2511	1964
Olifants	376	1977
Pafuri	846	1973
Phalaborwa	896	1975
Pretoriuskop	8320	1902
Punda Maria	1349	1919
Satara	3203	1913
Shangoni	2213	1958
Shingwedzi	4177	1904
Skukuza	2727	1902
Stolznek	575	1976
Tshokwane	6838	1928
Vlakteplaas	277	1978
Woodlands	74	1982
Total	**59757**	

Undergraduate University of Natal (Durban) students under my supervision entered the monthly predator return lion sightings onto separate spreadsheets for each section. The spreadsheets detailed the number of lions seen in each sex and age group, the date, location (grid reference and place name) and additional comments. I checked every single student's entries against the returns for errors. In addition, I read through the monthly ranger diaries to access additional

data, which were recorded onto spreadsheets as above. Separate spreadsheets were created for each station.

All the data from the returns and diaries were combined into one spreadsheet for each station. This was sorted according to date. The entries were checked for duplicates and where a sighting had been recorded in both the returns and diary, the information was combined to obtain the most detailed entry and the duplicate entry deleted.

The two methods used for the recording of sighting locations on the monthly predator returns included the use of a location descriptor and grid reference or a location descriptor only. Two types of grid reference were used. The first type refers to the management blocks. In 1957, when prescribed burning was introduced, KNP was divided into over 400 blocks, which range in size from 50 to 23 800ha (Van Wilgen, Biggs, O'Regan & Marè 2000). The blocks were labelled according to the district in which they occurred (N = northern, C = central, S = southern) and numbered. The second reference system used on the returns recorded a block reference such as 2431BC which referred to a 225min^2 block on the 1: 250 000 map. I also checked the location descriptors against the list of place names compiled by the former head of Nature Conservation, J.J. Kloppers, in which he listed the place names and their 225min^2 block locations. The location information was used to determine one min^2 block reference locations on a detailed 1:250 000 map of the KNP (Appendix 1.2). Entries where a river name was given were not used unless the entry had a grid reference or there was only one area where the river crossed a road. Where a location could not be found on the map, the location given was too vague, covered a large area, or fell on a farm outside KNP, the entry was deleted. The block reference system used to determine the locations on the 1: 250 000 map corresponded to the grid cell identifiers of an index map (Appendix 1.2; generation of index map detailed in Appendix 1.3).

Thus I determined the grid cell locations of the sightings and entered these into the spreadsheets for each station. After the deletion of duplicate entries and those entries for which grid cell locations could not be obtained, the remaining data totalled 46 940 sighting entries. The number of entries varied over the years, with a maximum of 2 970 entries in 1965 and a minimum of 558 entries in 1957 (Fig. 1.2).

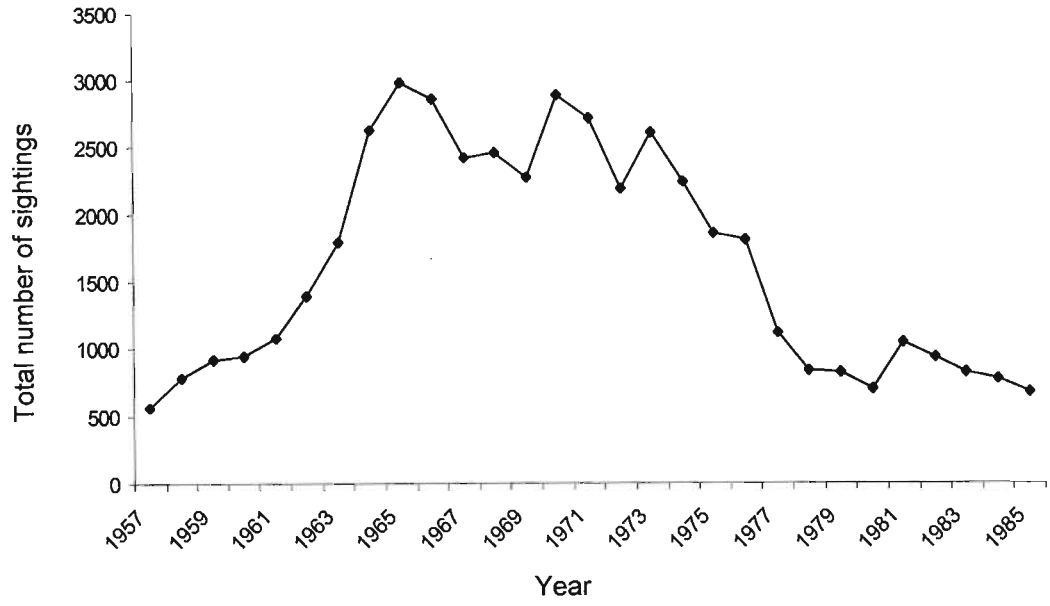

Figure 1.2. The number of lion sightings recorded each year. Only those sightings for which map locations could be determined have been used.

Lion variables

I decided to work with adult males in mixed groups and exclusively adult male groups. The adult males in mixed groups reflect the male coalitions that hold a pride, whereas the adult males alone will either account for males without a pride, or those males away from their pride. The amount of time males spend with their pride or away from their pride may give an indication of the number of males in their area. If males spend most of their time with the pride, this could indicate that there is a large number of competing males in the area, therefore the males are remaining with the pride to defend their females and cubs. It may also indicate that females in the area are in oestrus.

I separated the adult females into those that occurred in mixed groups and exclusively female groups. There is fission and fusion in prides where some females may leave the pride or join it depending on the conditions at the time (Packer *et al.* 1990). Generally, the same females will leave the pride together resulting in the formation of subgroups. My data of sightings of adult females alone may indicate females that have separated into subgroups or females that are hunting; while adult females in mixed groups are either with males (mating) or they have accompanying cubs and/ or subadults.

As very few sightings differentiated between female and male subadults, I decided to combine these data together with the data of unidentified subadults and investigate the total subadult

group size. The number of cubs in an area is a reflection of the productivity of that habitat, with the ratio of cubs to adult females indicating the individual fitness inferred by that habitat.

To summarise, the following variables were determined for Chapters Two to Four:

1. adult males in:
   1.1. mixed groups
   1.2. exclusively adult male groups
2. ratio of the number of sightings of males in mixed groups to exclusively adult male groups (Chapter Two only)
3. adult females in:
   3.1. mixed groups
   3.2. exclusively adult female groups
4. adult sex ratio (Chapter Two only)
5. cubs
6. cub to adult female ratio
7. subadults
8. total group size

Lions live in fission-fusion groups (Schaller 1972; Packer *et al.* 1990) where the pride splits into smaller subgroups that will group and separate over time. Therefore I decided to calculate the average and maximum lion variables. Average group size therefore reflects the size of the subgroups (from hereon referred to as groups) that lions form, while maximum group size may be a closer approximation of pride size.

The maximums, averages and number of sightings were calculated for variables one, three, five, seven and eight above. Variables two, four and six were calculated from data generated from variables one, one and three and three and five, respectively.

In Chapter Five, I worked with the maximum total adult group size, maximum exclusively adult male group size, maximum exclusively adult female group size and maximum cub group size. I used the total adult group size as a measure of the functional group size.

I produced maps for each lion variable for each short-term period using an index map as a reference map and assigning the variable value of each cell to a cell number on a blank map (the index map determines the placement of the value in space on the map).

The short-term period differed between chapters, in Chapter Two I used three-month periods (January-March, April-June, July-September, October-December) for the period from January 1957 to December 1985. As discussed in the section of data bias in this chapter, I averaged the data over three-month periods to reduce temporal pseudoreplication. I chose three-month periods in order to maximise the amount of data available for analysis. In Chapter Three, I used the data for the three-month period from July to September from the years 1978 to 1985. This corresponds to the year (1978) when full aerial surveys were first conducted and the year (1985) when the predator monthly returns were stopped. I used the data from July to September as this corresponds to the dry period when the aerial censuses are carried out. As rainfall is largely confined to the summer months (September to April) (Gertenbach 1980), I calculated the annual rainfall from 1 July to 30 June for each rainfall year from July 1957 to June 1985. Therefore in Chapter Four, I calculated the maximum and average lion variables over one-year periods from 1 July - 30 June and over six-month periods (April – September and October – March) from July 1957 to July and September 1985 for the two periods, respectively. In Chapter Five, I worked with the lion data in wet (October – March) and dry seasons (April – September) from 1978 to 1985. I averaged the data separately for each season.

I only worked with the adult sex ratio in Chapter Two. It was calculated per short-term period by determining the ratio of the maximum adult males to maximum adult females recorded, regardless of whether these adult lions were in mixed or exclusive groups (Appendix 1.4A). The ratio of maximum cubs to maximum adult females was also calculated per short-term period. The method used to determine the cub to female ratio was similar to that used to determine the adult lion sex ratios (Appendix 1.4B).

The variable maps for each of the short-term periods were added and averaged to obtain final maps for each variable for the entire period for each chapter. In Chapter Two the data were averaged over the 29-year period (January 1957 – December 1985), in Chapter Three the data were averaged over the eight-year period (1978 – 1985) and in Chapter Four over the 28-year period (July 1957 – June 1985). The resultant lion variable maps consisted of averaged average, averaged maximum or averaged ratio values for each cell. Hereafter, averaged average and averaged maximum are referred to as average and maximum, respectively.

As I worked with 116 files for each variable in Chapter Two, for ease of manipulation, I worked with the data in four groups (seasons) defined by the three-month periods. I added the variable maps for each of the four three-month periods to obtain one map per season. I created macro

files to increase the efficiency of this process (e.g. Appendix 1.5). These four maps were then added and averaged to obtain one final map for each lion variable for the entire 29-year period. This was also executed using macro files (e.g. Appendix 1.6). There were only eight final maps per variable in Chapter Three and one set of 28 annual variables maps and a second set of 56 seasonal variable maps per variable in Chapter Four. Therefore, I ran the map additions and averaging in one macro for each full period separately for each chapter.

Specific methods are detailed and discussed further in each chapter.

The lion variable files used in the analyses of each chapter are contained in Appendix X, the compact disk. The files are Idrisi version 2.0 raster images with their associated documentation files. Details for each folder of files are given on the disk.

Data Bias

Unfortunately, the nature of the data is such that there are many biases. The data are biased as a result of observer differences, some rangers giving more detailed information than others. This extends to the diaries, where some rangers recorded all their sightings while others recorded sightings less frequently. However, part of this difference may be explained by the fact that lions are not prevalent in all sections. The amount of information given by the observers also differs.

There is also visibility bias as, depending on the bush density an observer can only see a certain distance into the bush, which might create a bias when sampling open versus closed habitat types. However, the section and field rangers often went on specific transect drives/patrols to determine animal whereabouts, numbers etc on a regular basis. Therefore, they would have been more observant than someone merely looking for animals close to the road side. If lions were in an area, even if they were not seen on that day, they would likely be seen within a few days, as they would make a kill. The data are also not meant for fine analysis. They are to be used for broad scale patterns, therefore problems with visibility and possible ranger bias should not have a significant effect on the results.

Another problem arises as the data contain multiple sightings of the same lions, i.e. pseudoreplication (Hurlbert 1984). Pseudoreplication occurs when either the treatments in an experiment are not repeated. although samples may be, or as is the case with my project, when replicates are not statistically independent (Hurlbert 1984), i.e. the same lions are being counted

as independent data points. The problem of pseudoreplication arises in the data, as there are very few sightings with individual lion identification. If the sightings included identifications, multiple sightings could be reduced. However, as this is not the case, the data were either averaged or the maximum determined for specific time periods (see below). The problem of pseudoreplication occurs in the generation of the data points themselves, therefore by averaging the data (or using the maximum) and only using one datum based on multiple sightings per grid cell in the final analyses, the problem is not carried forward into the analyses themselves.

Where the same lions have been re-sighted and recorded as such, the shortest interval between sightings was one day and the longest three years. Intervals of 1, 1.5, 2, 3, 4 and 5 months were also noted between sightings of identified lions. However, not all of the re-sightings were at the exact same location. Most were often in the same vicinity, but, some were up to 6km apart. To reduce the pseudoreplication a period over which to average data had to be chosen. Different time periods were used depending on the analysis carried out and these are detailed in each chapter. I further reduced pseudoreplication by separately averaging, over the entire period, all the average and maximum data from each of the short time periods to produce a database that consisted of grid cells with one line of data per cell.

I worked with the data on a grid cell basis, which leads to a problem of spatial pseudoreplication as the same lions could be seen in adjacent cells. However, as I worked with the data averaged firstly over periods (e.g. three-month periods in Chapter Two) and secondly, those results averaged over 29 years, the data in adjacent cells should not be affecting each other. I did, however, investigate a method of random grid generation that would, for example, only use the data in cells at least ten cells distance apart. I investigated a simple procedure of random grid generation using the data in cells either five or ten cells distance apart, but these methods resulted in a drastic reduction in data used for analysis. In both cases, less than 5% of the possible cells to be used for analyses contained data.

Another problem arose as I used the same data set to generate a number of variables for analysis. These variables were not all independent of each other, therefore resulting in the same data being used in multiple tests. For example, I looked at the group sizes of adult males when males are both with other lions and in exclusively adult male groups. As I do not have individual identification data, I could not separate between the sightings of the same males when these males are either with females or in purely adult male groups. This resulted in the data concerning the same males being used in two tests. To overcome this problem, and reduce

the resultant type I error (rejecting the null hypothesis when it is true; Zar 1999), I applied the Bonferroni adjustment to the critical significance levels used in each analysis where this problem arose (Schork & Remington 2000). As a large number of variables were used in the analyses in each chapter, a major reduction in the critical significance level results. The consequence of this is a possible increase in the type II error, i.e. accepting the null hypothesis when it is false (Zar 1999). There is thus a trade-off between reducing the type I error through the Bonferroni adjustment and increasing the type II error. The most rigorous statistical procedure would involve dividing 0.05 by the total number of tests to determine the critical P value, for example, in Chapter Two 16 tests are performed which would result in a critical P value of 0.003. This statistical rigour would cloud the biological significance of the results. I therefore compromised by adjusting the critical P value for sets of tests that shared the same biological basis. For example, the number of tests involving adult males was summed, and the critical value for those tests were all divided by the summed total to give a more rigorous Bonferroni adjusted critical P value. The adjustments made to the significance levels used for analysis are discussed in each chapter.

Further data biases are discussed in the chapters in which they are relevant.

CHAPTER 2
THE EFFECT OF HABITAT STRUCTURE ON LION GROUP DYNAMICS

Introduction

The interaction of certain biotic and abiotic factors results in a particular habitat structure, where habitat structure refers to the physical appearance of the area. Physical appearance is determined by factors such as the openness of the area, the amount of cover and the topography. These variables have been found to affect the densities and activities of the organisms inhabiting the area when studied on a small or large scale (Schaller 1972; Bond, Ferguson & Forsyth 1980; Rowe-Rowe & Meester 1982; Van Orsdol 1984; Gotceitas & Colgan 1989; Tilman 1994).

Habitat selection is based on both the abiotic and biotic characteristics of a habitat (Warrick & Cypher 1998). The altitude, gradient, water availability and climate of an area are examples of the abiotic factors that will influence habitat selection (Bond *et al.* 1980; Rowe-Rowe & Meester 1982; Ritter & Bednekoff 1995). Biotic factors include the quality, quantity and distribution of a food supply, the density and distribution of intra- and interspecific competitors and the distribution and density of predators.

The optimal habitat not only provides for all of an animal's requirements in terms of energy intake but must also provide protection from, or allow for the avoidance of, predators and, provide protection from the elements (Pienaar 1974; Mills 1982; Christensen & Persson 1993). A habitat should provide protection for young. This is important, especially for lions, where new males taking over a pride will kill young cubs to induce oestrus in the females (Pusey & Packer 1994). In the case of lions, a good habitat provides females with suitable, hidden areas where their young cubs will be safe from infanticidal males and from leopards and hyaenas that prey on the cubs.

A good habitat should also allow for either, the coexistence of competitive species, or provide freedom from excessive competition (Pienaar 1974; Sih 1980; Hughes, Ward & Perrin 1994). This applies to both predators and prey species. Predators may have overlaps in their diets, competing for the same prey species (Mills & Biggs 1993). Competition for prey is affected not only by diet but also by the number of prey available and the relative number of predators. The habitat structure can affect the level of intraspecific confrontation (Birney, Grant & Baird 1976). Mills & Biggs (1993)

found that the five major predators in the Kruger National Park selected different habitats based on habitat structure.

Habitat structure places a constraint on hunting and hunting success. While vegetation may serve to hide prey from predators, it can also increase predation risk by decreasing the prey's ability to escape from predators; running speeds will be lower in shrub than in open areas. Shrub cover is also associated with shorter predator-detection distances, which increases predation risk (Schooley, Sharpe & van Horne 1993). The height and density of the vegetation influence the ease with which lions can stalk their prey without being detected. Van Orsdol (1984) found that hunting success in grasslands increased with grass height up to 0.8m and success in bushveld increased with higher bush cover. Short grass provides few hiding places for stalking lions while tall grass and woodlands/thickets supply ample cover (Schaller 1972). Lions should therefore choose the areas in which hunting success is high.

Ideal free distribution (IFD) is a model that is used to explain the distribution of animals in an environment consisting of good and low quality habitats (Fretwell & Lucas 1970). It assumes that individuals are 'free' to settle in any patch and that individuals are 'ideal' in that they have perfect knowledge of resource profitability in the available patches. Initially individuals entering the area will settle in the good quality patch until a point is reached when the fitness payoff gained by settling in the patch of poorer quality is equal to that gained in the rich habitat patch (Krebs & Davies 1993). Although the assumptions of IFD cannot always be met in nature, it is a useful mechanism for explaining animal distribution through space.

The aim of this chapter was to determine the effect of habitat structure on lion spatial ecology. I hypothesised that the distribution of animals between habitats would be influenced by the quality of the habitats. One prediction of IFD is that there will be more individuals in the resource rich habitat than in the resource-poor habitat, i.e. that the ratio of animals in each patch will be equivalent to the resource ratio between patches. I tested this hypothesis by comparing lion group dynamics across four broad structural habitat types in KNP. Previous studies have highlighted the importance of open tree savanna and thickets to lions (Mills & Biggs 1993; Mills & Gorman 1997). Open tree savannas also correspond with buffalo habitat. I therefore predicted that the group size of lions would be greatest in open tree savanna and smaller in the mountainous and more closed habitat

types. I predicted that reproductive output (i.e. individual fitness) would also be greatest in the open tree savanna.

Methods

Creation of the habitat map

I created a map of four habitat types based on the physical structure of the habitat (Appendix 2.1, Fig. 2.1). I based the habitats on their physical qualities as it is this structure that affects such activities as ease of movement through an area, hunting, visibility and shelter/ cover. Open areas, e.g. grasslands, provide some cover for hunting when the grass is long, but will not be beneficial in terms of hiding places or protection for young cubs from other carnivores and adult male lions. Closed areas, while providing protected areas, may hinder hunting if the vegetation is very dense. In terms of visibility, mountainous areas allow the individual a greater view of its territory than that allowed to individuals in flat areas. The mountains or koppies (rocky outcrops) also supply good hiding places for young cubs. I chose four habitat types based on their degree of openness with topography as a secondary factor. The four habitats included (1) Thickets, (2) Woodland, (3) Mountainous and (4) Open tree savanna, the characteristics of which are summarised in Table 2.1.

Table 2.1. Characteristics of the four structural habitat types.

Habitat	Descriptor	Topography	Tree density	Field layer	Shelter	Ease of movement
1	Thickets	Flat	Extremely dense	Sparse	High	Low
2	Woodlands	Flat	Moderate - dense	Moderate - dense	Medium	Medium
3	Mountainous	Broken	Open - dense	Moderate - dense	High	Medium
4	Open tree savanna	Flat	Few, scattered trees	Dense	Low - medium	High

Gertenbach (1983) separated the KNP into 35 landscape types, which were based on the specific geomorphology, climate, soil and vegetation pattern together with its associated fauna. I classified the 35 landscapes into the four structural categories (Table 2.2) mentioned above, in consultation with KNP botanists, Dr Gertenbach and Mr Potgieter. This permitted me to determine which physical habitats the lions were selecting and if this selection affected the group size or group composition.

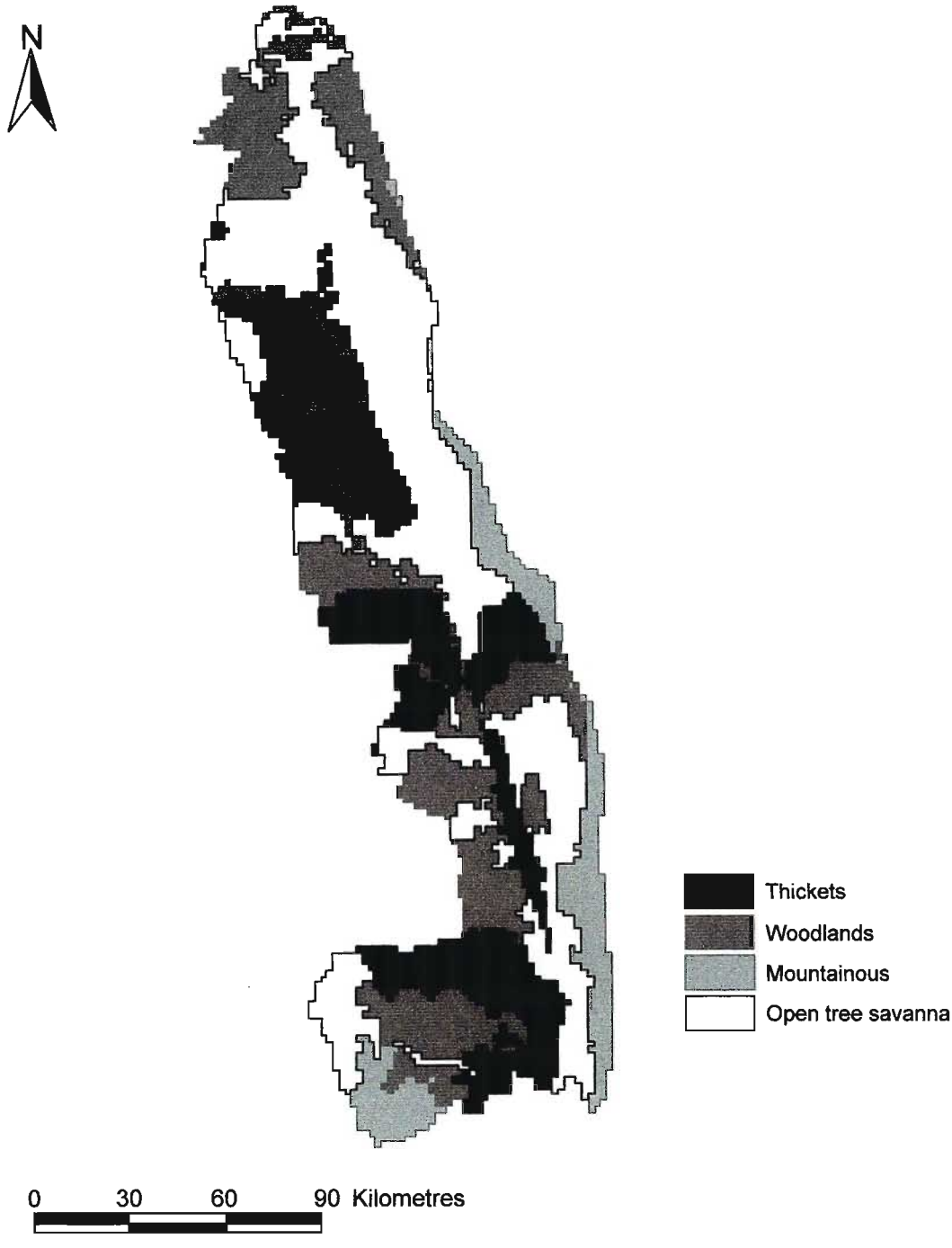

Figure 2.1. Structural habitat map of KNP created by reclassification of Gertenbach's landscape map (1983) into four habitats types based on physical structure. The map has a grid cell size of one minute^2.

Table 2.2. Summary comparison of Gertenbach's (1983) landscapes and the new values I assigned to create the structural habitat map used in analyses.

Gertenbach's number	Gertenbach's habitat classification	Habitat type	Habitat classification
1	Lower Sour Bushveld of Pretoriuskop	Open tree savanna	4
2	Malelane Mountain Bushveld	Mountainous	3
3	*Combretum collinum*/ *Combretum zeyheri* Woodland	Woodlands	2
4	Thickets of the Sabie and Crocodile Rivers	Thickets	1
5	Mixed *Combretum* spp. *Terminalia sericea* Woodland	Woodlands	2
6	*Combretum* spp./*Colophospermum mopane* Woodland	Thickets	1
7	Olifants River Rugged Veld	Thickets	1
8	Phalaborwa Sandveld	Woodlands	2
9	*Colophospermum mopane* Savanna on Basic Soils	Open tree savanna	4
10	Letaba River Rugged Veld	Thickets	1
11	Tsende Sandveld	Thickets	1
12	*Colophospermum mopane*/ *Acacia nigrescens* Savanna	Open tree savanna	4
13	*Acacia welwitschii* Thickets on Karoo Sediments	Thickets	1
14	Kumana Sandveld	Woodlands	2
15	*Colophospermum mopane* Forest	Woodlands	2
16	Punda Maria Sandveld on Cave Sandstone	Woodlands	2
17	*Sclerocarya caffra*/ *Acacia nigrescens* Savanna	Open tree savanna	4
18	Dwarf *Acacia nigrescens* Savanna	Woodlands	2
19	Thornveld on Gabbro	Open tree savanna	4
20	Bangu Rugged Veld	Thickets	1
21	*Combretum* spp./ *Acacia* spp. Rugged Veld	Thickets	1
22	*Combretum* spp./ *Colophospermum mopane* Rugged Veld	Thickets	1
23	*Colophospermum mopane* Shrubveld on Basalt	Open tree savanna	4
24	*Colophospermum mopane* Shrubveld on Gabbro	Woodlands	2
25	*Adansonia digitata*/ *Colophospermum mopane* Rugged Veld	Open tree savanna	4
26	*Colophospermum mopane* Shrubveld on Calcrete	Woodlands	2
27	Mixed *Combretum* spp. / *Colophospermum mopane* Woodland	Woodlands	2
28	Limpopo/ Levubu Floodplains	Woodlands	2
29	Lebombo South	Mountainous	3
30	Pumbe Sandveld	Woodlands	2
31	Lebombo North	Mountainous	3
32	Nwambia Sandveld	Woodlands	2
33	*Pterocarpus rotundifolius*/ *Combretum collinum* Woodland	Woodlands	2
34	Punda Maria Sandveld on Waterberg Sandstone	Woodlands	2
35	*Salvadora angustifolia* Floodplains	Open tree savanna	4

The area of each habitat was calculated in kilometres squared using the area function in IDRISI (Appendix 2.2). The percentage of the total area covered by each habitat was calculated. Not all the habitats have the same visibility, cover an equal proportion of KNP or have equal accessibility. The four habitats make up different proportions of the reserve (Fig. 2.1), with the mountainous category covering the smallest area (9.7% of reserve area, Table 2.3) and the open tree savanna covering the largest percentage area (37.8%, Table 2.3).

The probability of an area being sampled was dependent on the road coverage and therefore it was also non-random as the areas were mainly sampled along the roads. The road types include all roads open to the public as well as management tracks. The area of road coverage in each habitat was calculated based on a map with grid cell size of approximately 0.72km² that provided a 400 metre buffer area of visibility along both sides of the roads (Appendix 2.2, Table 2.3). A G-test was performed to test for significant differences in coverage. There was a significant difference (G-test: $G_{0.001,3} = 100.8513$; $P < 0.001$) in the proportion of road coverage in each habitat. However, this does not include the footpaths. It only accounts for the habitat accessible by vehicles. It also does not take into account that some roads will be used more often than others will. This adds in a further non-random sampling bias as the same roads may be used on a more regular basis as they form the shortest path to a destination.

Table 2.3. I determined the area covered by each of the four habitats (km²), the percentage each habitat covered of the total area of KNP (19 045 km²) as displayed on the habitat map and the area covered by roads in each habitat type.

Habitat	Habitat area (km²)	Percentage cover (%)	Area of habitat covered by roads (km²)[a]	Percentage cover (%)
Thickets	5208	27.3	1007	19.3
Woodlands	4792	25.2	1341	28.0
Mountainous	1839	9.7	467	25.4
Open tree savanna	7206	37.8	1949	27.0

[a] Area within approximately 400m either side of the road.

However, it is not only the difference in area and road coverage that may bias data but also visibility, which should differ between the four habitats as a result of the openness or density of the vegetation. To determine the importance of this problem, in September 1999, I used a range finder to measure the distance into the bush at which a one metre tall object could be seen from the road. I chose this time of year, as it would be the woody vegetation structure that would have more of an influence on visibility, as grass height should be constant throughout the park. A minimum of 6 transects was carried out in each habitat type on the roads between the Mopani rest camp and the Crocodile river (Fig. 2.2). Distance measurements were recorded on both sides of the road every 100m, for 400m starting at zero metres. This resulted in five readings for each side (Table 2.4). A minimum of 5km was driven between transects. The five readings measured were averaged for each side of the road for each transect. As the data were not normally distributed (Kolmogorov-Smirnov test, $P < 0.001$) I log-transformed the data and compared the distances in each habitat using ANOVA (Zar 1999). There was no significant difference between the average distances measured

for each habitat (ANOVA: $F_{3,98} = 1.913$; $P = 0.133$). However, when I determined the variance in the averaged distances measured for each habitat for both sides of the road combined, the open tree savanna had the greatest variance, while the thickets had the lowest (Table 2.5).

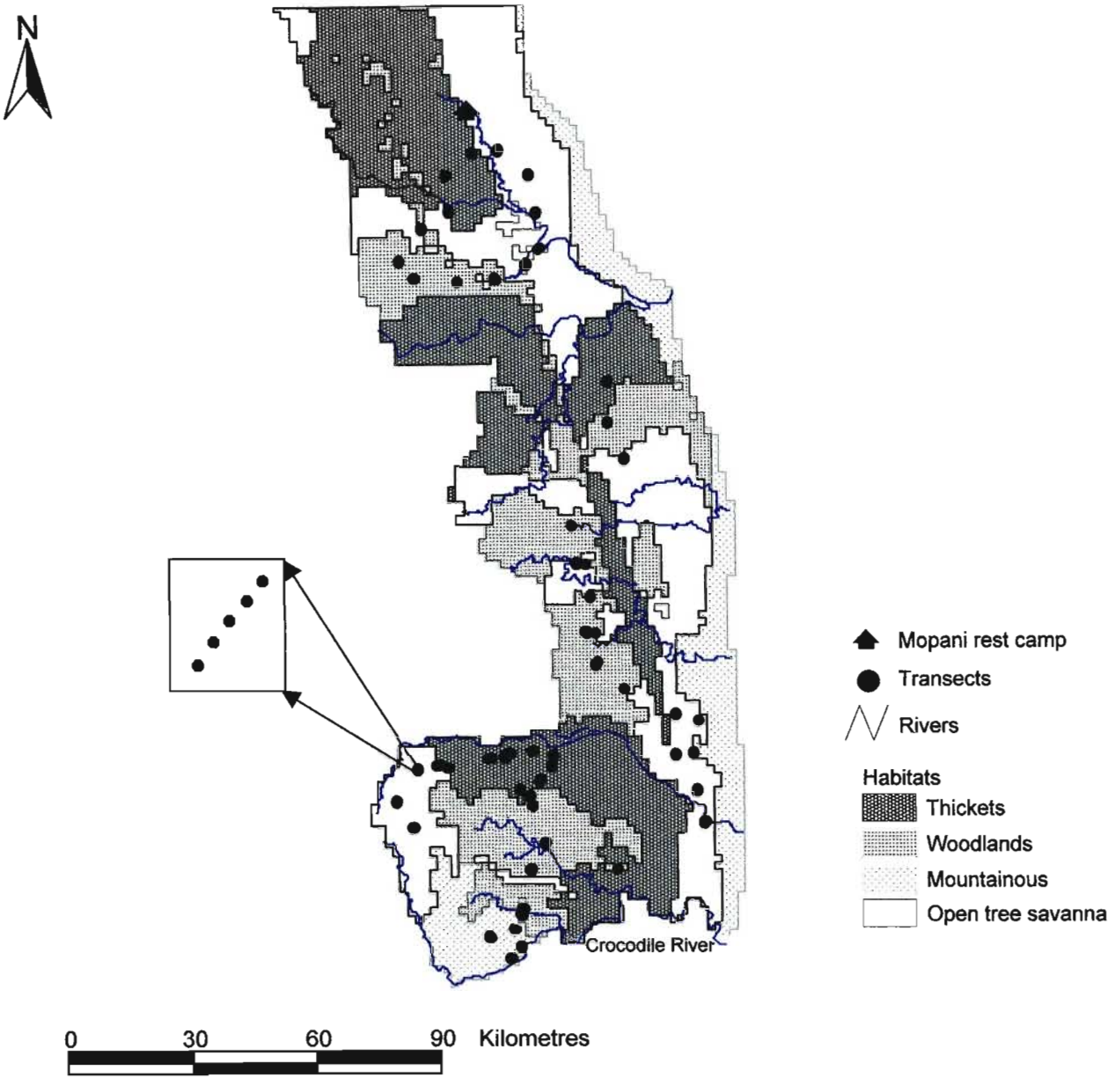

Figure 2.2. The distance at which a one metre object could be seen from the road was measured in transects in all four habitat types between the Crocodile River in the south and the Mopani rest camp in the north. Each dot on the main map represents the five places sampled in each transect. The map has a grid cell size of one minute².

Table 2.4. I tested the visibility among habitat types by comparing the distance into the bush that a one metre high object could be seen from the road. The distance measurements from the road into the bush were averaged for each side of the road resulting in two distance measurements for each transect, one to the left and one to the right of the vehicle.

Transect No.	Habitat	Distance to left (m)	Distance to right (m)
1	Thickets	65.8	53.2
2	Thickets	81.9	51.0
3	Thickets	65.9	79.5
4	Thickets	52.6	57.5
5	Thickets	14.8	5.0
6	Thickets	36.5	31.0
7	Thickets	29.7	22.9
8	Thickets	76.2	41.8
9	Thickets	84.8	82.0
10	Thickets	158.0	170.0
32	Thickets	79.1	151.7
37	Thickets	36.0	33.5
38	Thickets	23.6	41.2
21	Woodlands	43.6	37.9
22	Woodlands	77.5	77.3
23	Woodlands	55.7	32.0
30	Woodlands	202.4	195.9
31	Woodlands	108.7	101.6
33	Woodlands	19.0	16.0
41	Woodlands	72.7	112.8
42	Woodlands	47.0	33.7
43	Woodlands	22.0	37.0
44	Woodlands	15.0	14.6
45	Woodlands	46.4	57.9
46	Woodlands	95.4	110.2
49	Woodlands	84.3	137.5
50	Woodlands	60.4	68.4
51	Woodlands	68.0	77.7
15	Mountainous	51.9	60.1
16	Mountainous	63.5	408.5
17	Mountainous	29.4	54.0
18	Mountainous	69.2	168.8
19	Mountainous	117.9	76.7
20	Mountainous	52.4	50.1
11	Open tree savanna	367.4	154.5
12	Open tree savanna	52.9	86.3
13	Open tree savanna	56.8	19.1
14	Open tree savanna	27.6	43.0
24	Open tree savanna	44.6	68.5
25	Open tree savanna	93.3	90.9
26	Open tree savanna	147.5	530.1
27	Open tree savanna	484.4	411.3
28	Open tree savanna	177.3	84.6
29	Open tree savanna	27.1	54.3
34	Open tree savanna	56.8	213.0
35	Open tree savanna	83.4	156.3
36	Open tree savanna	32.6	41.1
39	Open tree savanna	10.0	10.6
40	Open tree savanna	69.3	49.4
47	Open tree savanna	96.0	105.1
48	Open tree savanna	74.9	119.4

Table 2.5. The habitat variance between the averaged distance measurements into the bush increased with increasing bush openness.

Habitat	Variance
Thickets	1793.4
Woodlands	2272.7
Mountainous	10801.0
Open tree savanna	18511.6

Lion variables

I divided the files created for each station into three-month periods for each year from January 1957 to December 1985 (January-March, April-June, July-September, October-December)(details of data, data capture and preparation are to be found in the general methods section of Chapter One). The data from every station were combined for each three-month period resulting in 116 three-month periods. The average, maximum and number of sightings of each variable for each grid cell was calculated over this period resulting in one line of data for each block reference. Lions live in fission-fusion groups (Packer *et al.* 1990). Therefore I calculated both the average and maximum group sizes, as the average group size should be a reflection of the subgroups, while the maximum should be a closer approximation of pride size. The average and maximum data were averaged over three-month periods to reduce the problem of pseudoreplication (Hurlbert 1984; pseudoreplication discussed further in Chapter One).

I decided on a time period of three months as an initial duration for the following reasons. Time periods of six-months or one-year were investigated, but as with the data in the three-month periods mentioned above, many cells had only one recorded sighting. The other option would involve using subsets of data and leaving out periods in between. However, while this reduces the amount of data for analysis, it does not decrease pseudoreplication. Hence it was decided to maximise the data used and determine the average and maximum over three-month periods. Gus Mills[1] (pers. comm.) stated that even if lions are seen in the same place two days in a row, unless they are at a kill, they could have moved away from the area during the night to hunt and returned to the same spot the following day. This would then serve as two independent points as the lions have chosen to return to the area. Pseudoreplication was also reduced by the fact that the data from each three-month period was also averaged over the 29-year period for final analyses, i.e. the analyses are based on one data set of all the data averaged. This resulted in averaged average and averaged maximum lion variables for the final analysis.

Visibility is potentially a problem as it differs between each season depending on the grass length and bush density. Therefore another advantage is gained by working with the three-month periods (January-March, April-June, July-September, October-December), namely that the four periods encompass the four seasons and so there should be no difference in the visibility experienced within

[1] Dr M.G.L. Mills, Scientific Services, Private bag X 402, Skukuza, 1350, tel.: (013) 7354240.

that period. In general, the number of sightings recorded in each season did not vary from year to year (Fig. 2.3) and there was no significant difference between the number of sightings recorded in each season when I tested this using ANOVA (ANOVA: $F_{3,112} = 0.844$; $P = 0.472$).

Visibility does not only differ between seasons but it, together with cover, will also vary between years as a result of fluctuating rainfall. This factor is investigated further in Chapter Four.

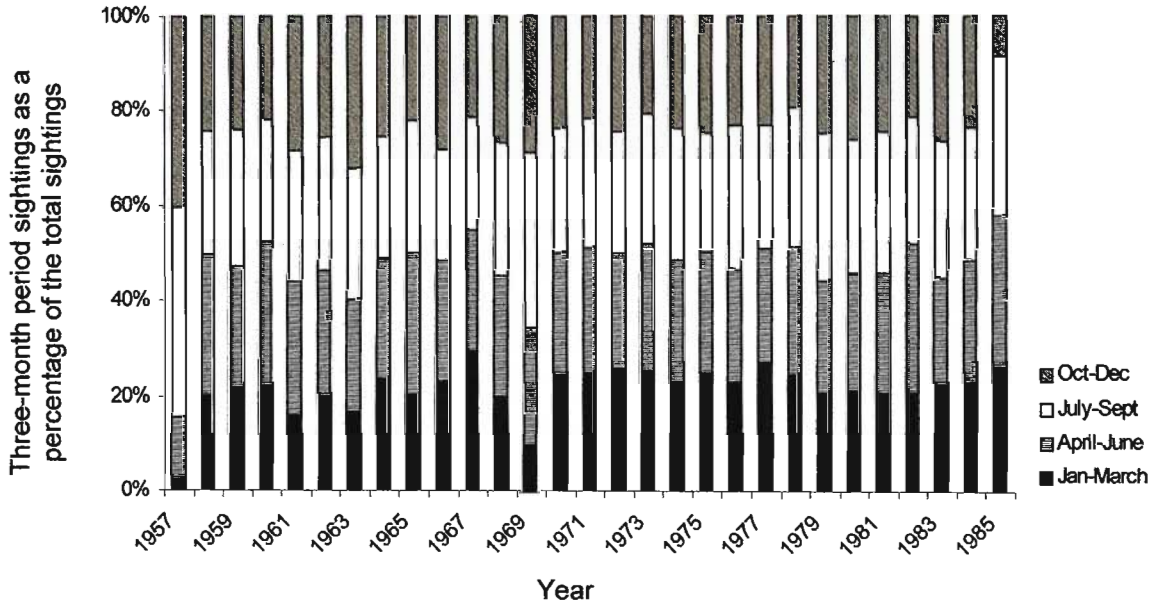

Figure 2.3. The distribution of the number of sightings in the four periods/ seasons as a percentage of the total recordings of each year was similar over the 29-year period. Only those sightings for which map locations could be determined have been used.

If habitat structure affects group size and group composition, then these factors should differ between open and closed habitats. I worked with the following lion variables (details are given in Chapter One):

1. adult males in:
   1.1. mixed groups
   1.2. exclusively adult male groups
2. ratio of the number of sightings of males in mixed groups to exclusively adult male groups
3. adult females in:
   3.1. mixed groups
   3.2. exclusively adult female groups

4. adult sex ratio
5. cubs
6. cub to adult female ratio
7. subadults
8. total group size

The maximums, averages and number of sightings were calculated for variables one, three, five, seven and eight. Variables two, four and six were calculated from data generated from variables one, one and three and three and five, respectively. I produced variable maps for each three-month period (116 maps per lion variable).

The 116 files for each variable were added and averaged which resulted in 17 lion variable maps that had averaged average, averaged maximum or averaged ratio values for each cell (Details are presented in Chapter One). Hereafter, averaged average and averaged maximum are referred to as average and maximum, respectively. The number of sightings for each lion variable was totalled for each habitat for the entire period.

To test the IFD hypothesis I compared the lion variables between the four structural habitat types. I extracted the data from each of the final 17 variable maps for further analyses (Appendix 2.3). As the data were not normally distributed (Kolmogorov-Smirnov test $P < 0.05$ in all cases), a Kruskal-Wallis one-way ANOVA was used to compare the variables in each habitat type (Zar 1999). The test variables were one of 17 dependent variables and the grouping variable was habitat type (minimum = 1 [thickets], maximum = 4 [open tree savanna]).

The difference between the four habitats in the ratio of total number of sightings of adult males in mixed groups to adult males alone was compared using the Kruskal-Wallis one-way ANOVA (Zar 1999).

I applied the Bonferroni adjustment to the significance levels used for each variable because the same data were used for multiple tests (Schork & Remington 2000). For each variable I calculated the P value as 0.05 divided by the number of tests that that variable and related variables had been used for (Table 2.6)(See Chapter One for details).

Box-and-whisker plots showing the median, first and third quartiles and the range were used to illustrate the data. As the patterns shown by the average and maximum data were similar, I have only illustrated the maximum data. Although, outliers and extremes were used in the analyses I have not represented them in the box plots in order to avoid cluttering and to facilitate interpretation of trends.

To determine which habitats were most favourable. the total number of variable sightings in each habitat were compared using G-tests (Zar 1999). This was done based on habitat area and the road area and is represented by bar graphs. I also adjusted the critical significance levels for interpretation of the results (i.e. Bonferroni adjustment, Schork & Remington 2000; Table 2.6).

Table 2.6. I adjusted the critical significance levels for the lion variables used in the Kruskal-Wallis one-way ANOVA and the categorical analyses based on the number of tests that each variable was used in or not independent of. Thus for each group size and sightings variable I included those tests for which the total group sizes or total group sightings were used, respectively.

Variable	Tests	Number of tests	P [a]
Adult male group sizes	Average and maximum adult males in mixed groups, average and maximum exclusively adult male group sizes, adult sex ratio, average and maximum total group sizes	7	0.007
Number of male sightings	Habitat and road area categorical analyses for adult males in mixed groups, exclusively adult males and total groups and male sightings ratio	7	0.007
Adult female group sizes	Average and maximum adult females in mixed groups, average and maximum exclusively adult female group sizes, adult sex ratio, cub: adult female ratio, average and maximum total group sizes	8	0.006
Number of female sightings	Habitat and road area categorical analyses for adult females in mixed groups, exclusively adult females and total groups	6	0.008
Adult sex ratio	Average and maximum adult males in mixed groups, average and maximum exclusively adult male group sizes, adult male ratio, adult sex ratio, average and maximum adult females in mixed groups, average and maximum exclusively adult female group sizes, cub: adult female ratio, average and maximum total group sizes	13	0.004
Subadult group sizes	Average and maximum subadult group sizes, average and maximum total group sizes	4	0.013
Number of subadult sightings	Habitat and road area categorical analyses for subadults and total group	4	0.013
Cub group sizes	Average and maximum cub group sizes, cub: adult female ratio, average and maximum total group sizes	5	0.01
Number of cub sightings	Habitat and road area categorical analyses for cubs and total group	4	0.013
Cub: adult female ratio	Average and maximum adult females in mixed groups, average and maximum exclusively adult females, average and maximum cub group sizes, adult sex ratio, cub: adult female ratio, average and maximum total group	10	0.005
Total group sizes	All the above mentioned variables related to group sizes	16	0.003
Total number of group sightings	All the above mentioned variables related to number of sightings	15	0.003

[a] P = Bonferroni adjusted critical P- level for significance testing (Schork & Remington 2000). P equals 0.05 divided by the number of tests.

Spatial patterns

I created continuous surface maps for each lion variable using the seven final averaged maximum group size data and the three sets of ratio data. I created maps for the adult males in mixed groups, exclusively adult male groups, male sightings ratio, adult females in mixed groups, exclusively adult female groups, adult sex ratio, subadult groups, cub groups, cub: female ratio and the total group sizes. I compared the distribution of the group sizes and ratios against the habitat map to see if the patterns of distribution varied in the four habitat types across KNP.

Results

Adult males in mixed groups

There was a significant difference between both the average and maximum group sizes of adult males in mixed groups among different habitats (Table 2.7). Although the difference was less marked for the maximum group sizes, the median group size of the mountainous areas was higher than that of the other habitats (Fig. 2.4). The woodlands had the greatest range in terms of the average and maximum group sizes recorded (Fig. 2.4).

The spatial pattern of group distribution across KNP showed that there were more groups of males than single males with mixed groups in the open tree savanna along the eastern section and in the south-western section, while there were more single males in the north-west (Fig. 2.8). There were mainly single males associating with mixed groups in the thickets in both the north and south of KNP (Fig. 2.8). There was approximately an equal distribution of both single males and groups of males in mixed groups in the woodlands and mountainous areas (Fig. 2.8).

The total number of sightings recorded in each habitat differed significantly based on both the habitat area and road coverage (Table 2.8). Based on habitat area more sightings than expected were recorded in the mountainous areas and open tree savanna, but based on road area there were more sightings than expected in the mountainous areas and thickets (Fig. 2.5). However, it must be noted that the mountainous areas occur along the boundaries of the reserve, which are areas patrolled more often by staff (Gus Mills[2], pers. comm.). The number of males occurring in mixed groups was generally greater in the more open habitats than in the thickets, i.e. the coalitions holding prides in more open areas tend to be larger than those with prides in closed areas.

Exclusively adult male groups

Based on the adjusted significance levels, there were no significant differences between the average group sizes of exclusively adult male groups (Table 2.7). The difference in the maximum group sizes recorded was not significant (Table 2.7), with a median of about 1.5 being recorded in all four habitat types (Fig. 2.4). There was little difference in the distribution of solitary males and coalitions in the thickets throughout KNP (Fig. 2.9). There were more solitary males in the open

[2] Dr M.G.L. Mills, Scientific Services, Private bag X 402, Skukuza, 1350, tel.: (013) 7354240.

tree savanna, woodlands and mountainous areas in the north and south-west, while this pattern was reversed in all habitats in the central and south-eastern areas (Fig. 2.9).

The difference in the total number of sightings recorded in each habitat over the 29-year period was significant when analysed in terms of both habitat and road area (Table 2.8). Based on habitat area, there were more sightings than expected in the mountainous areas and open tree savanna. However, when road area was used there were not only more sightings than expected in the mountainous areas and open tree savanna, but also in the thickets (Fig. 2.5). While there are smaller groups of exclusively adult males in the mountainous areas, there is little difference between the size and range in size of male lion groups in the other habitats. Exclusively adult male groups are choosing habitats where males in mixed groups occur, but with a slightly higher preference for the open tree savanna and slightly lower preference for the thickets than that calculated for males in mixed groups.

Number of sightings of adult males in mixed groups compared with those of exclusively adult male groups

In all four habitats there were more sightings of adult males in mixed groups recorded per cell than sightings per cell of groups consisting of adult males exclusively (Fig. 2.6). There was, however, no significant difference between the ratio of sightings of males in mixed groups compared to exclusively male groups between the four habitats (Table 2.7), a median of about 2.3 being recorded in all four habitats (Fig. 2.7). Although the ratio does not differ significantly between the habitats, it does imply that throughout the park adult male coalitions are spending the majority of their time with females or in mixed groups rather than alone. Based on the interpolated surface map of male sightings, there was little difference in the distribution of sightings of either male group in all four habitats throughout the park (Fig. 2.10).

Adult females in mixed groups

The differences between the average adult female group sizes in mixed groups and the maximum group sizes in different habitats was not significant based on the adjusted significance levels (Table 2.7; Fig. 2.4). Throughout KNP, regardless of habitat type, there were more groups of two to four females in mixed groups than either single females or larger groups, which indicates a preference for this group size (Fig. 2.11). This is in agreement with Packer *et al.* (1990), who found that

although groups of two to four were not optimal in terms of food acquisition, it was the preferred group size formed.

A significant difference between the number of sightings was found when both the habitat and road area were used in analyses (Table 2.8). In both cases more sightings than expected were recorded in the mountainous areas and open tree savanna. The woodlands and thickets had fewer than expected sightings for both their area and road coverage (Fig. 2.5). However, the difference recorded for the thickets was less when the road area was used as when the habitat area was used (Fig. 2.5). Adult females in mixed groups are therefore seen more often in the more open habitats of the mountainous areas and open tree savanna where they are present in larger groups. The mountainous areas may provide more protection for cubs and good cover for successful hunting. The open tree savanna, depending on the grass cover, will also supply good cover for hunting and good visibility of the surrounding areas.

Exclusively adult female groups

There were no significant differences between either the average or the maximum exclusively adult female group sizes recorded in the four habitats (Table 2.7; Fig. 2.4). There were more solitary females in the woodlands and thickets in north-western KNP than further south (Fig. 2.12). However, in the open tree savanna in the south-western section there were more solitary females than groups of females (Fig. 2.12). Adult females occurring in the south-eastern mountainous areas were generally in groups of two to four, while in the south-west and further north there was an equal distribution of solitary females and groups (Fig. 2.12).

As with the females in mixed groups, there were significantly more sightings than expected in the mountainous areas and open tree savanna based on habitat area and road coverage (Table 2.8; Fig. 2.5). There were more sightings than expected in the thickets, but based on road coverage only (Fig. 2.5). Groups consisting of adult females exclusively are therefore showing a similar habitat preference, the open habitats of the mountainous areas and open tree savanna, to adult females in mixed groups. Exclusively adult female groups may be selecting for habitats based on prey availability and cover for hunting.

Adult sex ratio

The adult sex ratio was calculated on a per-cell basis for the cells that contained both males and females. It did not differ significantly between the four habitats (Table 2.7), all four having a median ratio of less than one (ranged from 44 to 47% males). The averaged adult male to female ratio for the entire park did not differ significantly from a 50:50 ratio (G-test, $G_{0.05,1} = 0.811$, $P = 0.05$). There were generally more females than males, the ratios of 1♂: 8♀ to 1♂: 1.1♀ predominating throughout the park (Fig. 2.13).

Subadults

Analysis of the subadult data showed a significant difference between the average and maximum group sizes recorded in the four habitats (Table 2.7). For both variations of group size, the mountainous area reflected the lowest median average and maximum group sizes (Fig. 2.4). The woodlands and the open tree savanna had the largest group sizes while the thickets fell slightly below these two (Fig. 2.4). The median average group size was three in the woodlands and open tree savanna and about 2.5 for the thickets and 2.2 for the woodlands. The woodlands and open tree savanna areas also had the highest range in subadult group sizes, with groups of up to seven and more being recorded. As cub litters consist of an average of three cubs, the above medians would suggest a high survival rate if the subadults were from one litter but low if there were a few litters born in the pride. However, as initial cub litter sizes and numbers are not known, survival rates of the young lions cannot be inferred. Generally the female subadults remain with the pride while the males are evicted (Schaller 1972; Smuts *et al.* 1978; Anderson 1980; Hanby & Bygott 1987), which could also explain smaller subadult group sizes.

The spatial pattern of subadult group sizes across KNP showed a predominance of groups of one to three subadults in all habitats (Fig. 2.14). There were a few areas in the central and northern open tree savanna and woodlands where larger groups were present to a greater extent (Fig. 2.14).

Based on habitat and road area, there was a significant difference in the total number of sightings recorded in each habitat (Table 2.8). When the test was done using habitat area, there were more sightings than expected in the mountainous areas and open tree savanna (Fig. 2.5). However, when road area was used, there were fewer sightings than expected in all habitats except the mountainous (Fig. 2.5). Most of the subadult sightings occurred where the subadults were still with adult lions, which would explain their predominance in the same habitats as the adults. The larger subadult

group sizes in the woodlands and open tree savanna. however, indicate that these habitats may be more conducive to survival of young lions.

Cubs

The average and maximum cub group sizes showed significant differences among the habitats (Table 2.7). The woodlands had the highest median average group size, while the thickets and mountainous habitats had the lowest median maximum group sizes (Fig. 2.4). The median average and maximum cub group size was above three in the woodlands which implies that more than one litter was born into the pride while the other three habitats had median average group sizes of three and below.

Although there were mainly groups of one to three cubs throughout KNP, there were large areas of the open tree savanna and woodlands in the north and, the open tree savanna, woodlands and thickets in central KNP where larger groups (four to 12) were present (Fig. 2.15). These results indicate that the woodlands and open tree savanna areas have a higher absolute productivity, based on cub group size, than do the thickets and mountainous areas. However, there were significantly more cub sightings than expected in the mountainous areas and open tree savanna based on both habitat and road areas (Table 2.8; Fig. 2.5). Adult females in mixed groups were found predominantly in the mountainous areas and open tree savanna, which in relation to these results, suggests that the females are choosing these habitats because of the presence of cubs in the pride/ subgroup. The mountainous areas provide protection for cubs as well as cover for hunting, the open tree savanna provides good cover for hunting, while the thickets provide protection for cubs but may not be as advantageous for hunting. However, the woodlands have a high absolute productivity from which one could infer that it is a habitat that should be selected by lionesses with cubs.

Cub: adult female ratio

The cub: adult female ratio differed significantly (Table 2.7) with greater cub to female ratios recorded in the woodlands (Fig. 2.7). Although the cub ratio was generally between one and three cubs per adult female throughout the park, there were areas of low reproductive output (less than one cub per adult female) in the northern thickets and open tree savanna (Fig. 2.16). The fact that the ratio was generally greater than one throughout the park indicates that the relative productivity is good in all four habitats. However, as this ratio is based on a per-cell calculation and does not

take area and exact lion numbers into account the result cannot be used for generalisations about absolute productivity.

Total group size

There were no significant differences between the average or maximum total group sizes between the four habitats (Table 2.7). The median average and median maximum group size was about four (Fig. 2.4). Although there was little difference in the group sizes recorded in the four habitats, more sightings than expected were recorded in the mountainous areas and open tree savanna; while there were fewer than expected in the woodlands and thickets based on both habitat and road area (Table 2.8; Fig. 2.5). The lions therefore appear to be selecting for more open habitats where there may be good hunting success as a result of the cover provided by the vegetation and also increased visibility of the surrounding areas.

Larger groups of lions (five to 30) were predominant in the south-eastern and central open tree savanna and woodlands of KNP, with smaller groups predominating in the north, regardless of habitat type (Fig. 2.17). The mountainous areas and thickets in southern KNP had approximately equal distributions of both group size categories (Fig. 2.17).

Table 2.7. Resource-rich habitats should sustain larger groups than resource-poor habitats. Although there were differences between the group sizes recorded in the four structural habitat types, the differences were not always significant.

	Average		Maximum		Ratio	
Lion variable	χ^2	P	χ^2	P	χ^2	P
Adult males in mixed groups[a]	17.3	0.001	22.9	0.001		
Exclusively adult male groups[a]	9.0	0.029	7.4	0.059		
Males in mixed group: exclusively male groups[a]					3.3	ns
Adult females in mixed groups[b]	8.3	0.04	9.4	0.025		
Exclusively adult female groups[b]	6.7	0.083	7.3	0.06		
Adult sex ratio (max ♂ : max ♀)[c]					2.0	ns
Subadult group size[d]	16.1	0.001	12.8	0.005		
Cub group size[e]	12.6	0.006	12.2	0.007		
Cub: maximum adult female ratio[f]					13.1	0.004
Total group size[g]	6.3	0.097	4.7	ns		

Df = 3 in all cases.

Note: The critical significance levels have been adjusted as the data were used in multiple tests (Schork & Remington 2000). The adjusted critical P values are: [a] P = 0.007; [b] P = 0.006; [c] P = 0.004; [d] P = 0.013; [e] P = 0.01; [f] P = 0.005; [g] P = 0.003

Results where P >0.1 have been noted as ns (non-significant), although only results with P< critical value have been interpreted as significant.

Table 2.8. The number of lion observations in each structural habitat type was used as a measure of habitat selection. The categorical analyses were all significant, with more sightings than expected for all lion variables in the mountainous areas. Observations were also greater than expected in the open tree savanna for all variables except adult males in mixed groups.

	Habitat area		Road coverage	
Variable	G	P	G	P
Adult males in mixed groups [a]	27.9	0.001	34.6	0.001
Exclusively adult male groups [a]	1126.1	0.001	1113.5	0.001
Adult females in mixed groups [b]	3901.7	0.001	3759.5	0.001
Exclusively adult female groups [b]	254.6	0.001	265.6	0.001
Subadult group size [c]	603.7	0.001	265.6	0.001
Cub group size [c]	248.1	0.001	269.5	0.001
Total group size [d]	5012.2	0.001	4834.3	0.001

Df = 3 in all cases.

Note: The critical significance levels have been adjusted as the data were used in multiple tests (Schork & Remington 2000). The adjusted critical P values are: [a] P = 0.007; [b] P = 0.008; [c] P = 0.013; [d] P = 0.003

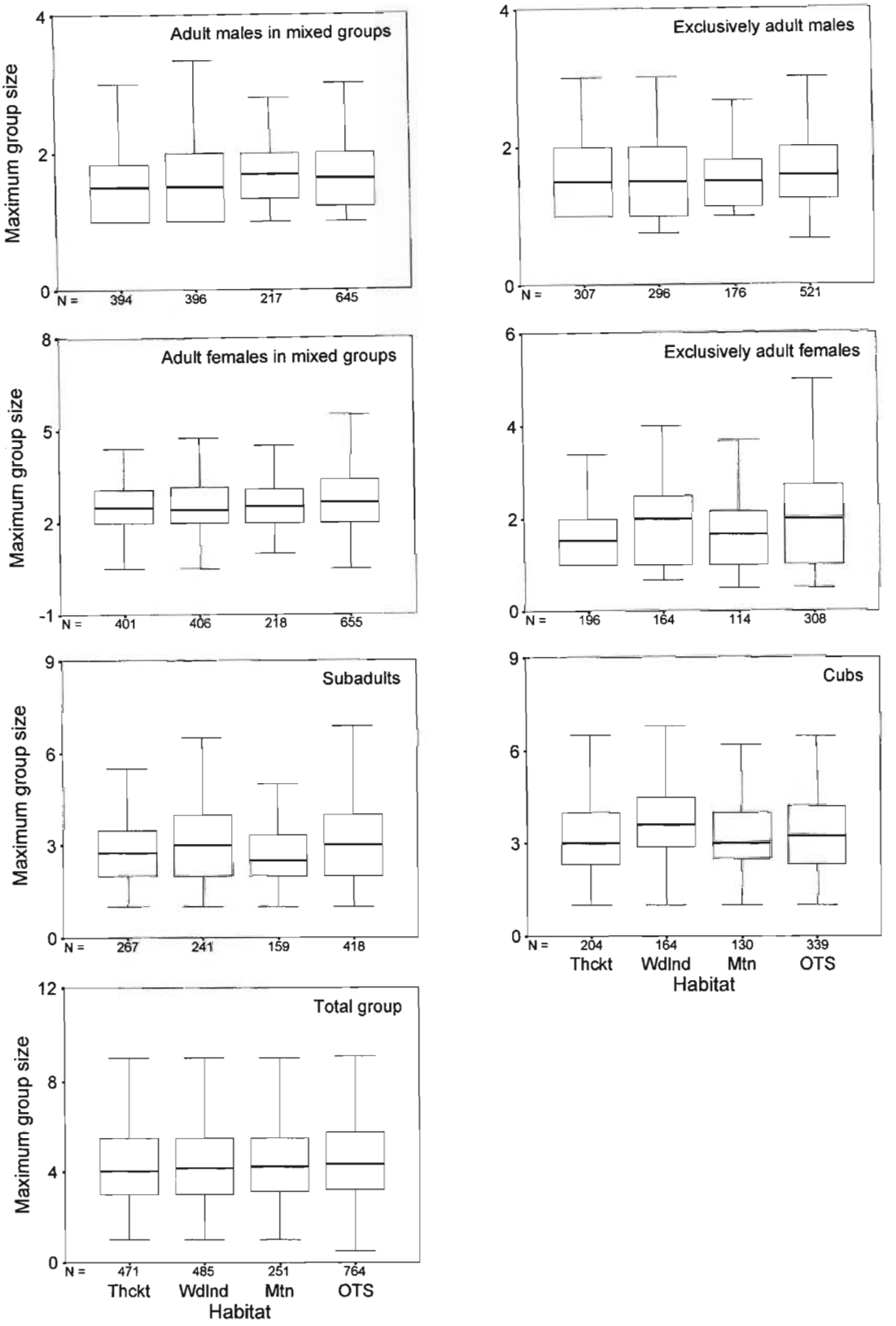

Figure 2.4. Habitat structure only resulted in significant differences between the groups sizes of adult males in mixed groups, subadults and cubs. I have only presented the box-and-whisker plots for the maximum lion variables as trends for the averaged variables are similar. The plots show the median, first and third quartiles and the range of the data. Outliers and extremes have been excluded. The habitat abbreviations used are (1) Thckt = thicket, (2) Wdlnd = woodlands, (3) Mtn = mountainous and (4) OTS = open tree savanna. N = number of one minute^2 cells with sightings.

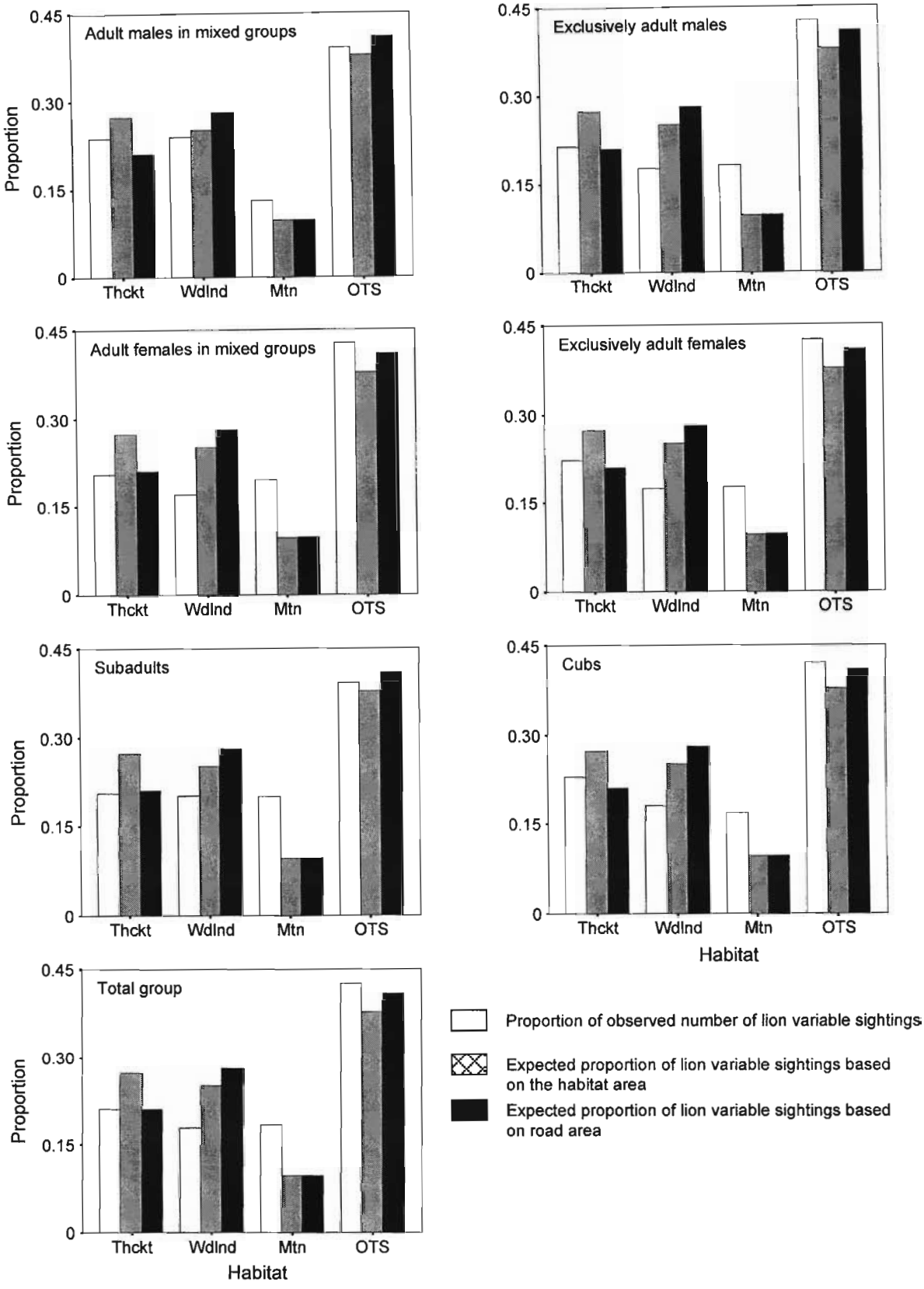

Figure 2.5. There were always more sightings than expected in the mountainous areas and in the open tree savanna (with the exception of adult males in mixed groups). The habitat abbreviations used are (1) Thckt = thicket, (2) Wdlnd = woodlands, (3) Mtn = mountainous and (4) OTS = open tree savanna.

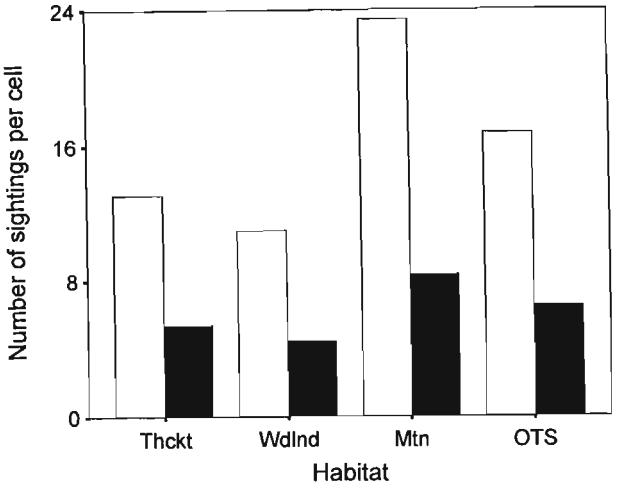

Figure 2.6. The mean number of sightings per cell of adult males in mixed groups (open bar) was greater than that recorded for exclusively adult male groups (solid bar) in all four habitats. The habitat abbreviations used are (1) Thckt = thicket, (2) Wdlnd = woodlands, (3) Mtn = mountainous and (4) OTS = open tree savanna.

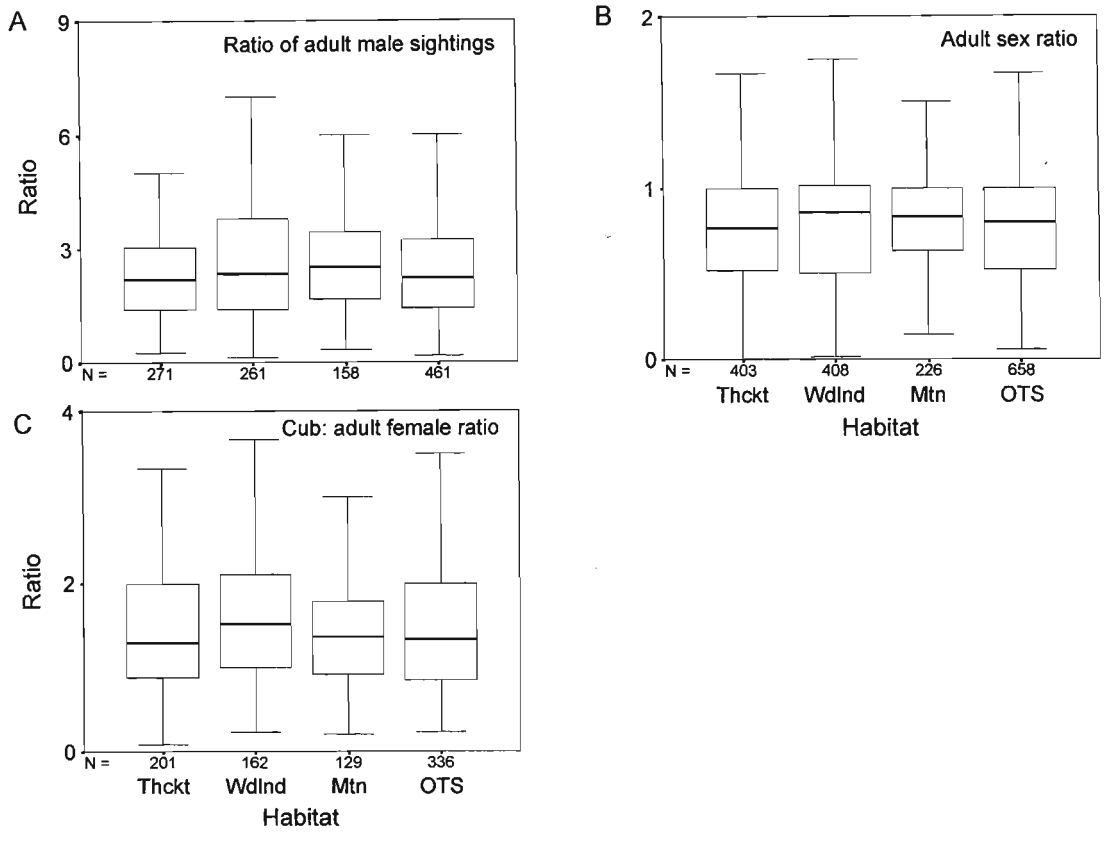

Figure 2.7. The ratio of adult male sightings (A) and the adult sex ratio (B) did not differ significantly between the four habitat types. However, the cub: adult female ratios differed, with the greatest median ratio recorded in the woodlands (C). The box-and-whisker plots show the median, first and third quartiles and the range of the data. Outliers and extremes have not been included. The habitat abbreviations used are (1) Thckt = thicket, (2) Wdlnd = woodlands, (3) Mtn = mountainous and (4) OTS = open tree savanna. N = number of one minute^2 cells with sightings.

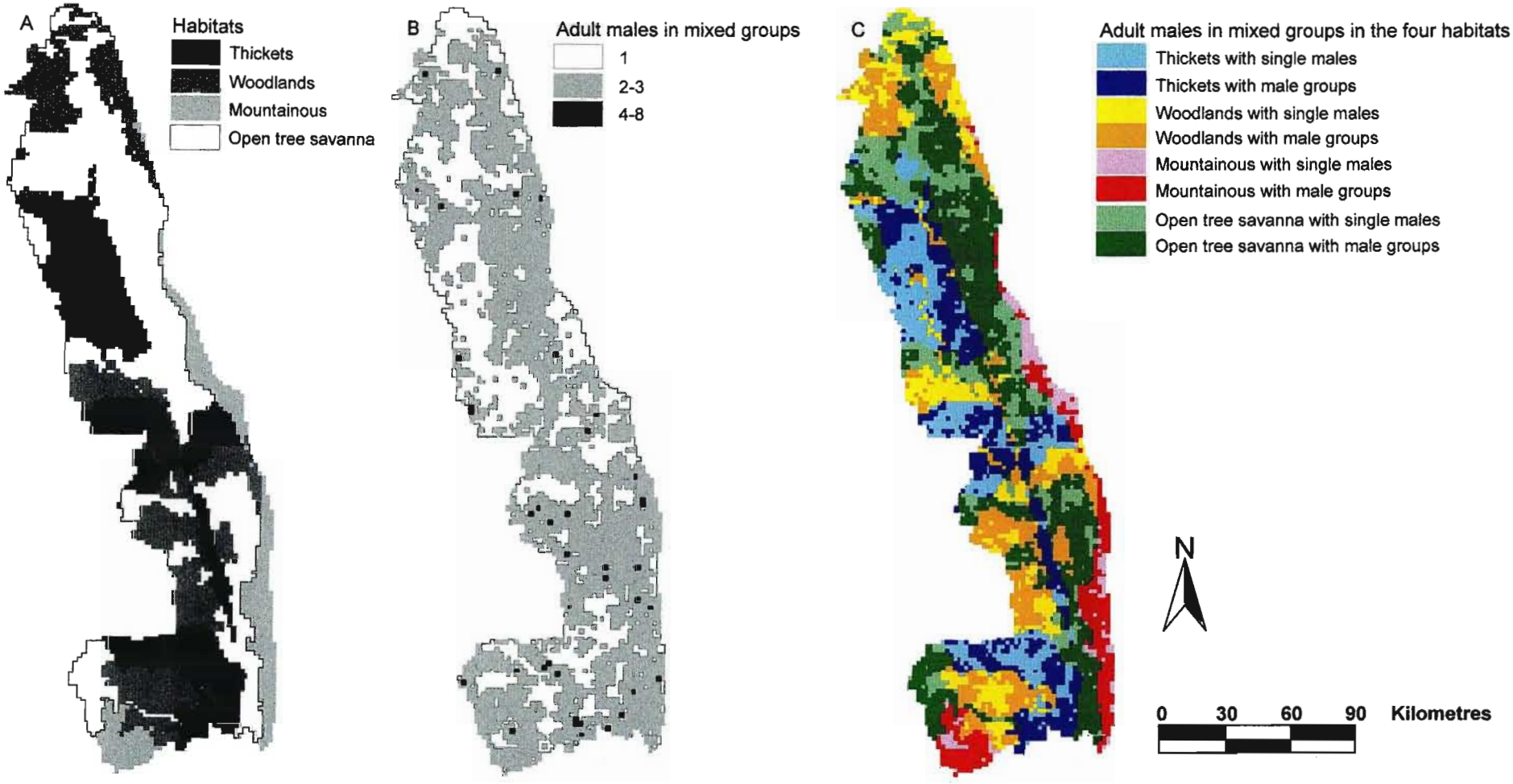

Figure 2.8. The surface map showing the distribution of maximum group sizes of adult males in mixed groups (B) was overlaid on the habitat map (A) to determine the spatial distribution of adult males in mixed groups through KNP (C). For ease of interpretation only two measures of group size were used for the map combining habitat and group size (C). In all habitat types there were more groups of males than single males associating with mixed groups (C). In the north-west and central western sections of KNP there appeared to be more single males than coalitions associating with mixed groups (C). The maps have a grid cell size of one minute².

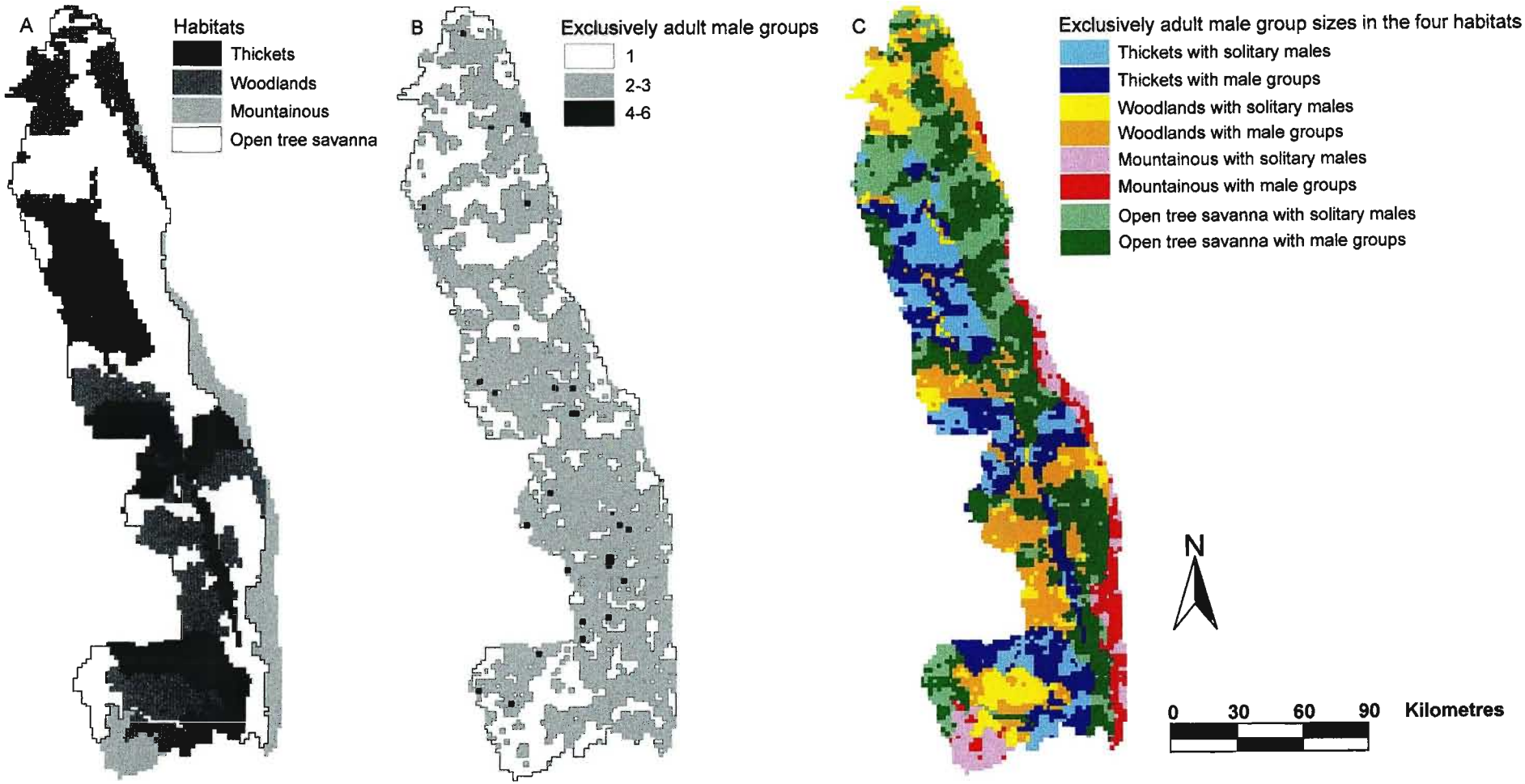

Figure 2.9. The surface map showing the distribution of maximum exclusively adult male group sizes (B) was overlaid on the habitat map (A) to determine the spatial distribution of exclusively adult male groups through KNP (C). For ease of interpretation only two measures of group size were used for the map combining habitat and group size (C). In the woodlands in central KNP there were more coalitions of males than solitary males, while in the north and south, there were more solitary males in the woodlands (C). This pattern was similar in the open tree savanna and mountainous areas, while there was little difference between the distribution of coalition sizes in the thickets in any area of KNP (C). The maps have a grid cell size of one minute².

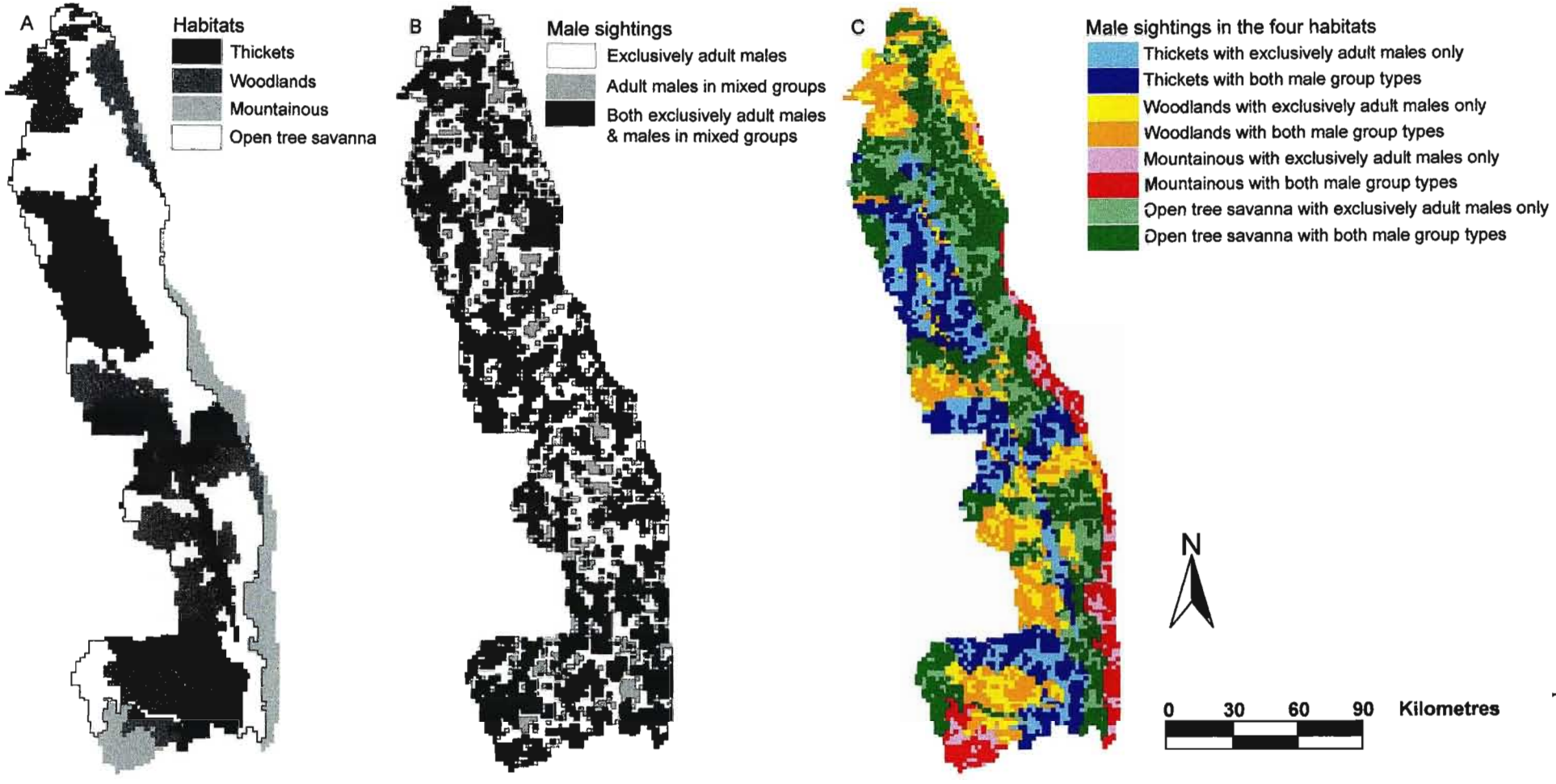

Figure 2.10. The surface map showing the distribution of sightings of exclusively adult males and adult males in mixed groups (B) was overlaid on the habitat map (A) to determine the spatial distribution of observations of adult males in mixed groups compared to that of exclusively adult male groups across KNP (C). For ease of interpretation only two measures of male sightings were used for the map combining habitat and male sightings (C). In all four habitat types there were more cells with sightings of both exclusively adult male groups and males in mixed groups than of exclusively adult male groups alone (C). The maps have a grid cell size of one minute².

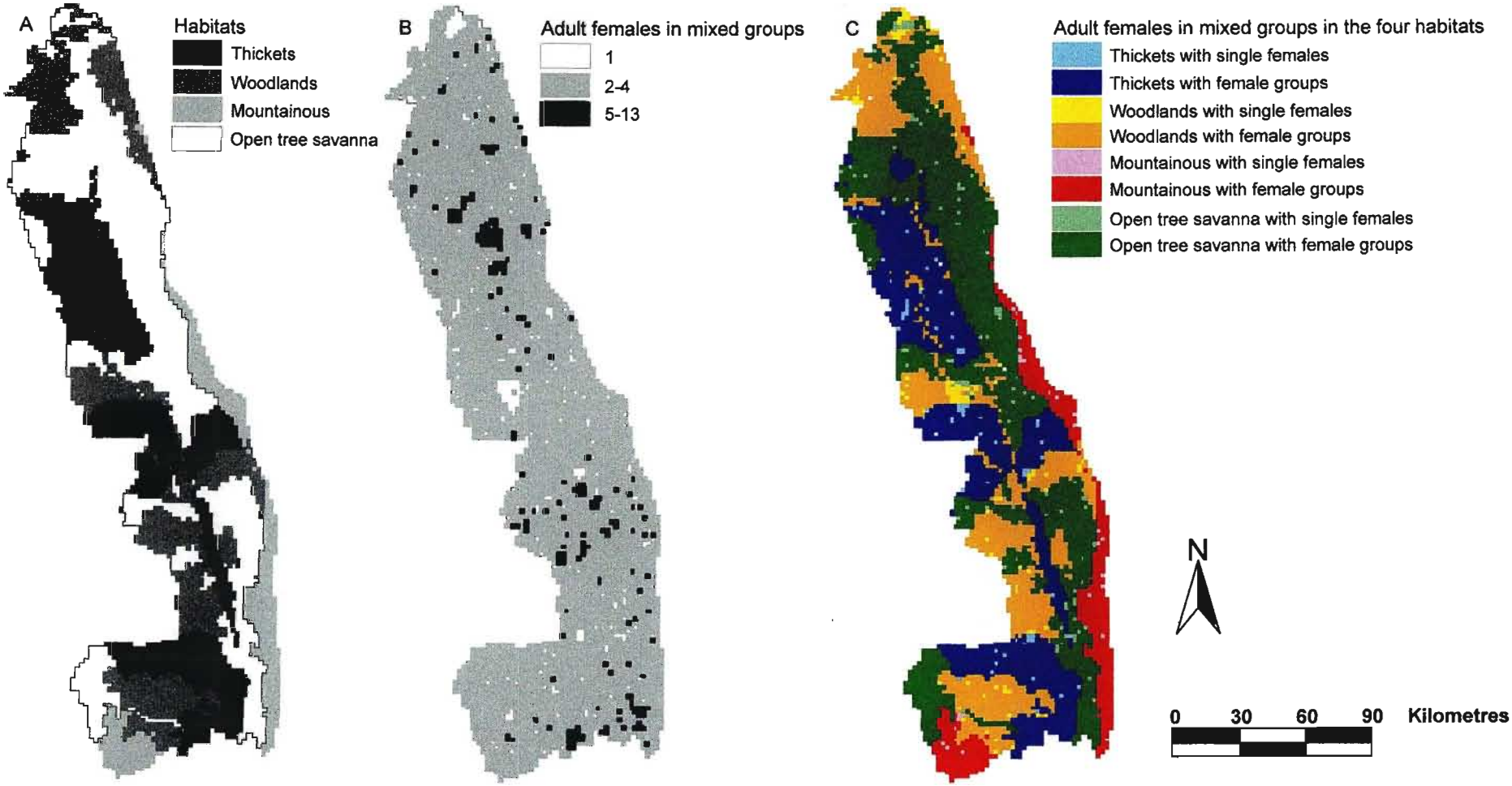

Figure 2.11. The surface map showing the distribution of maximum group sizes of adult females in mixed groups (B) was overlaid on the habitat map (A) to determine the spatial distribution of adult females in mixed groups through KNP (C). For ease of interpretation only two measures of group size were used for the map combining habitat and group size (C). Throughout KNP and in all habitat types there were more groups of females than single females (C). The maps have a grid cell size of one minute².

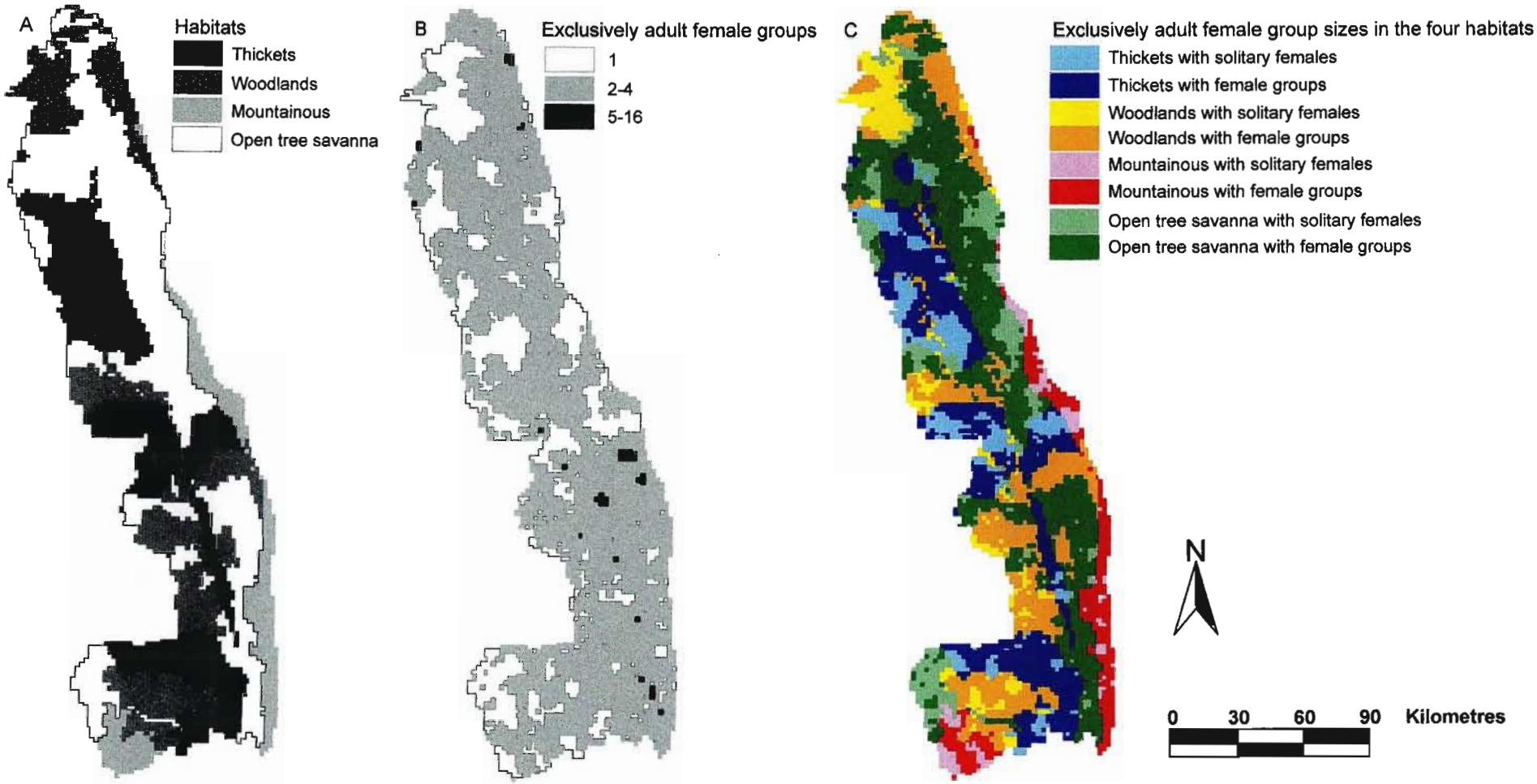

Figure 2.12. The surface map showing the distribution of maximum exclusively adult female group sizes (B) was overlaid on the habitat map (A) to determine the spatial distribution of exclusively adult female groups through KNP (C). For ease of interpretation only two measures of group size were used for the map combining habitat and group size (C). There were more solitary females in the woodlands and thickets in north-western KNP than in the woodlands and thickets further south (C). The open tree savanna in the south-western section of KNP had more solitary females than groups of females, this pattern was reversed in the south-eastern section while there was approximately an equal distribution of solitary females and groups of females in the open tree savanna further north (C). The maps have a grid cell size of one minute².

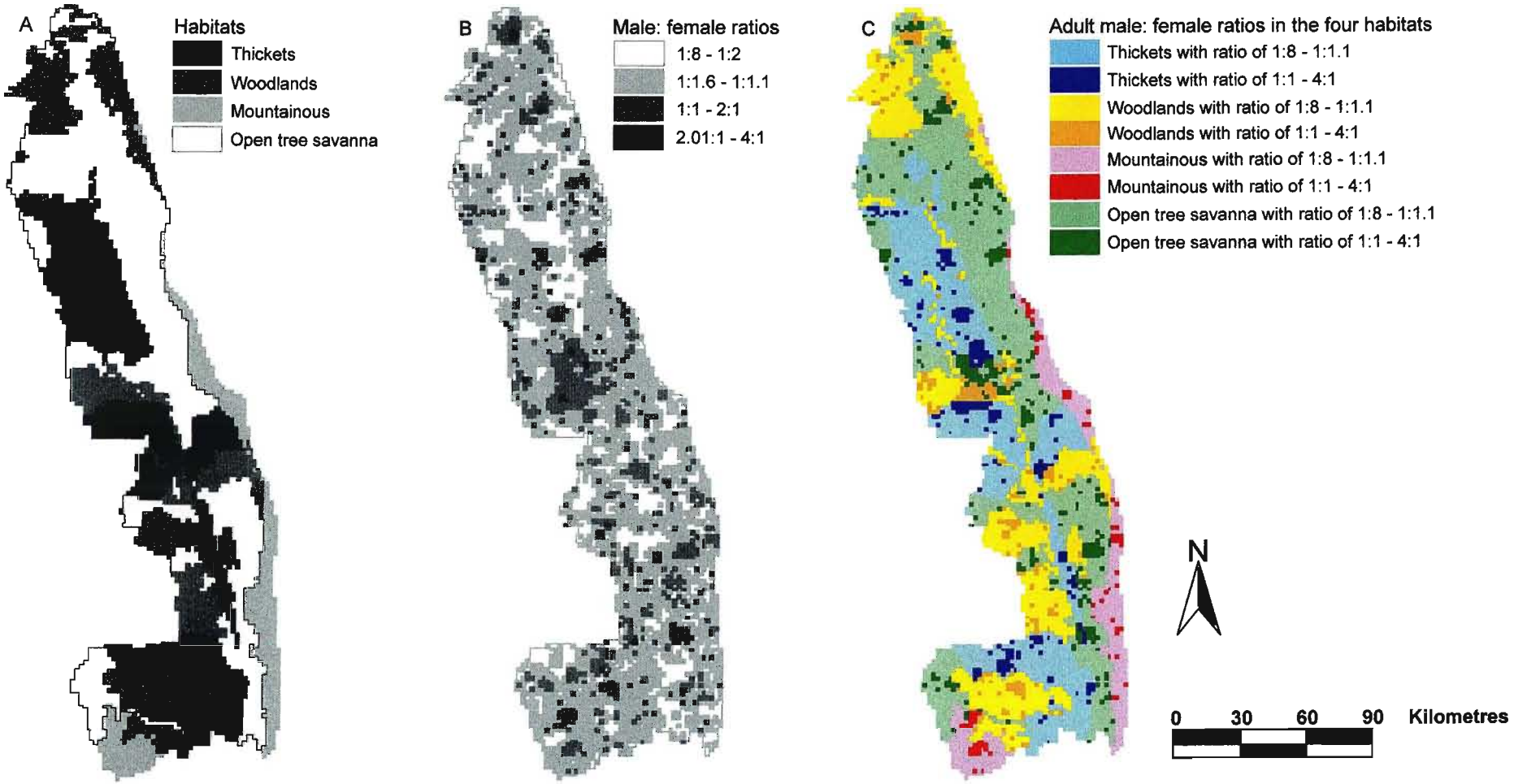

Figure 2.13. The surface map of adult male: female ratios (B) was overlaid on the habitat map (A) to compare the areas of male and female predominance (C). For ease of interpretation only two ratio categories were used for the map combining habitat and ratio (C). There were generally more females than males in the four habitats throughout the park (C). The maps have a grid cell size of one minute^2.

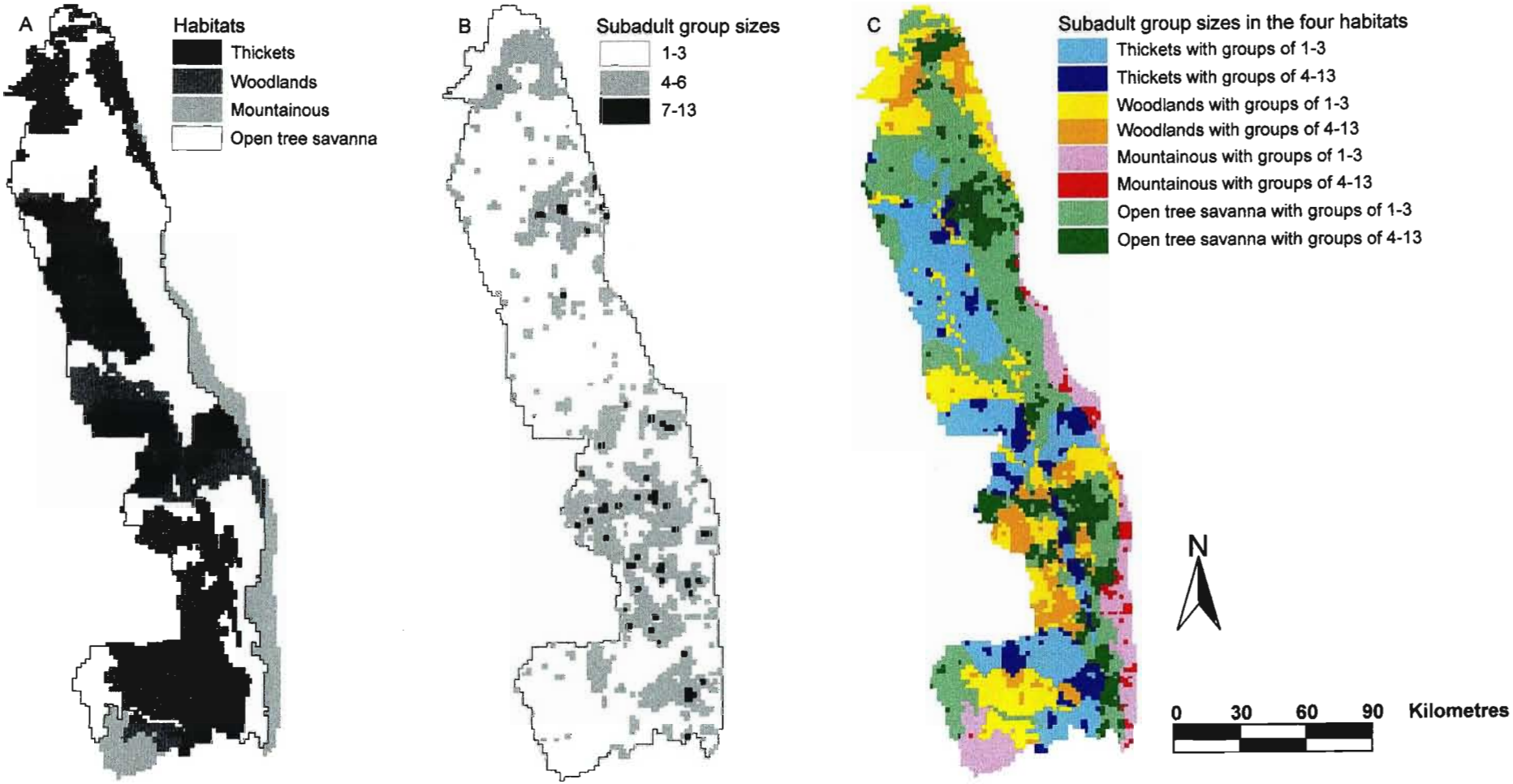

Figure 2.14. The surface map showing the distribution of maximum subadult group sizes (B) was overlaid on the habitat map (A) to determine the spatial distribution of subadult groups through KNP (C). For ease of interpretation only two measures of group size were used for the map combining habitat and group size (C). The majority of subadult groups throughout the park consisted of one to three individuals (C). There were a few areas in the northern and central woodlands and open tree savanna and the southern thickets where larger subadults groups (four to 13) were present (C). The maps have a grid cell size of one minute².

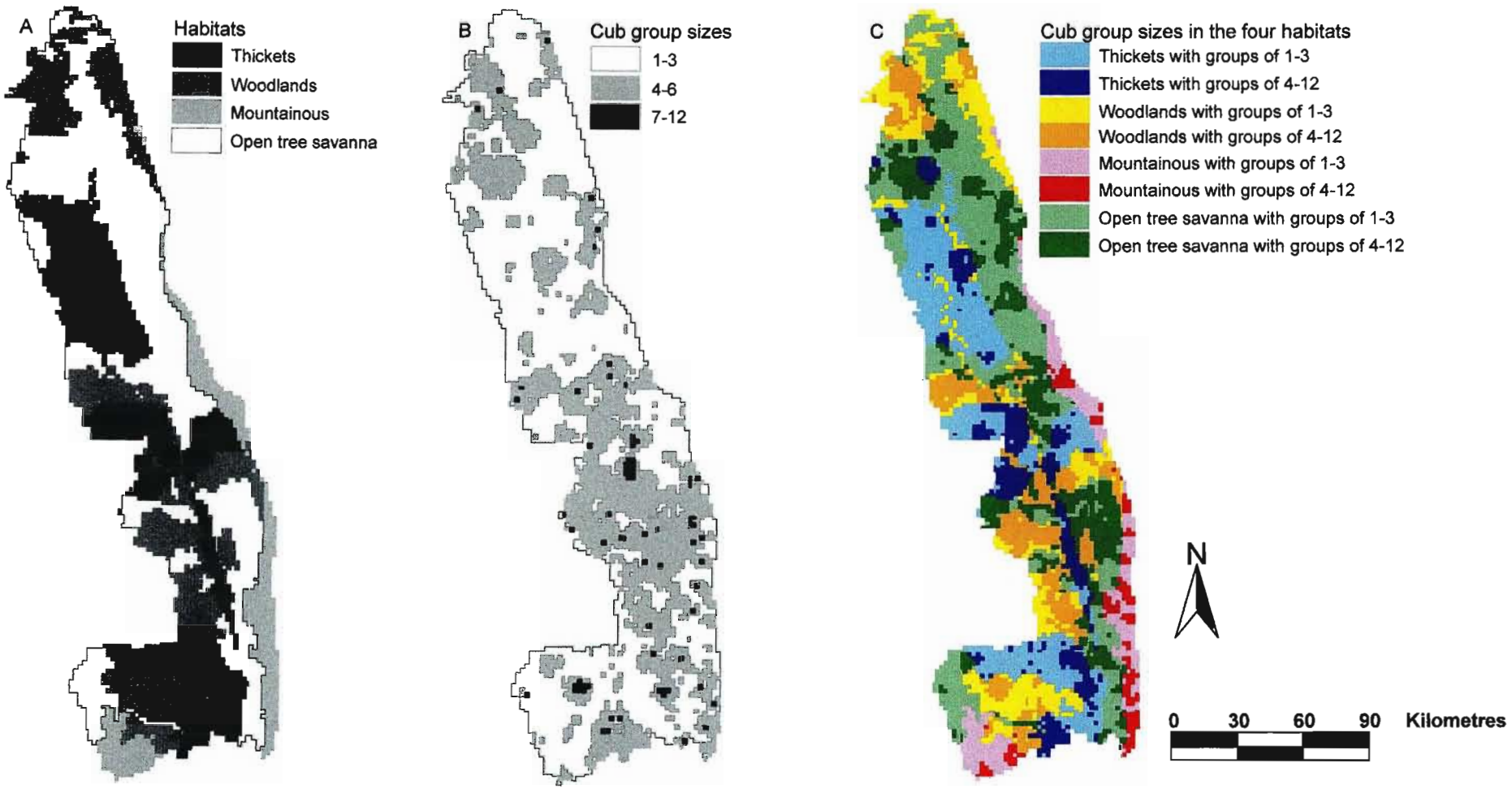

Figure 2.15. The surface map showing the distribution of maximum cub group sizes (B) was overlaid on the habitat map (A) to determine the spatial distribution of cub groups through KNP (C). For ease of interpretation only two measures of group size were used for the map combining habitat and group size (C). As with the subadult group distribution, the majority of groups throughout the park consisted of one to three cubs (C). Larger cub groups occurred in the thickets, woodlands and open tree savanna in central KNP and the woodlands and open tree savanna in the north (C). The maps have a grid cell size of one minute².

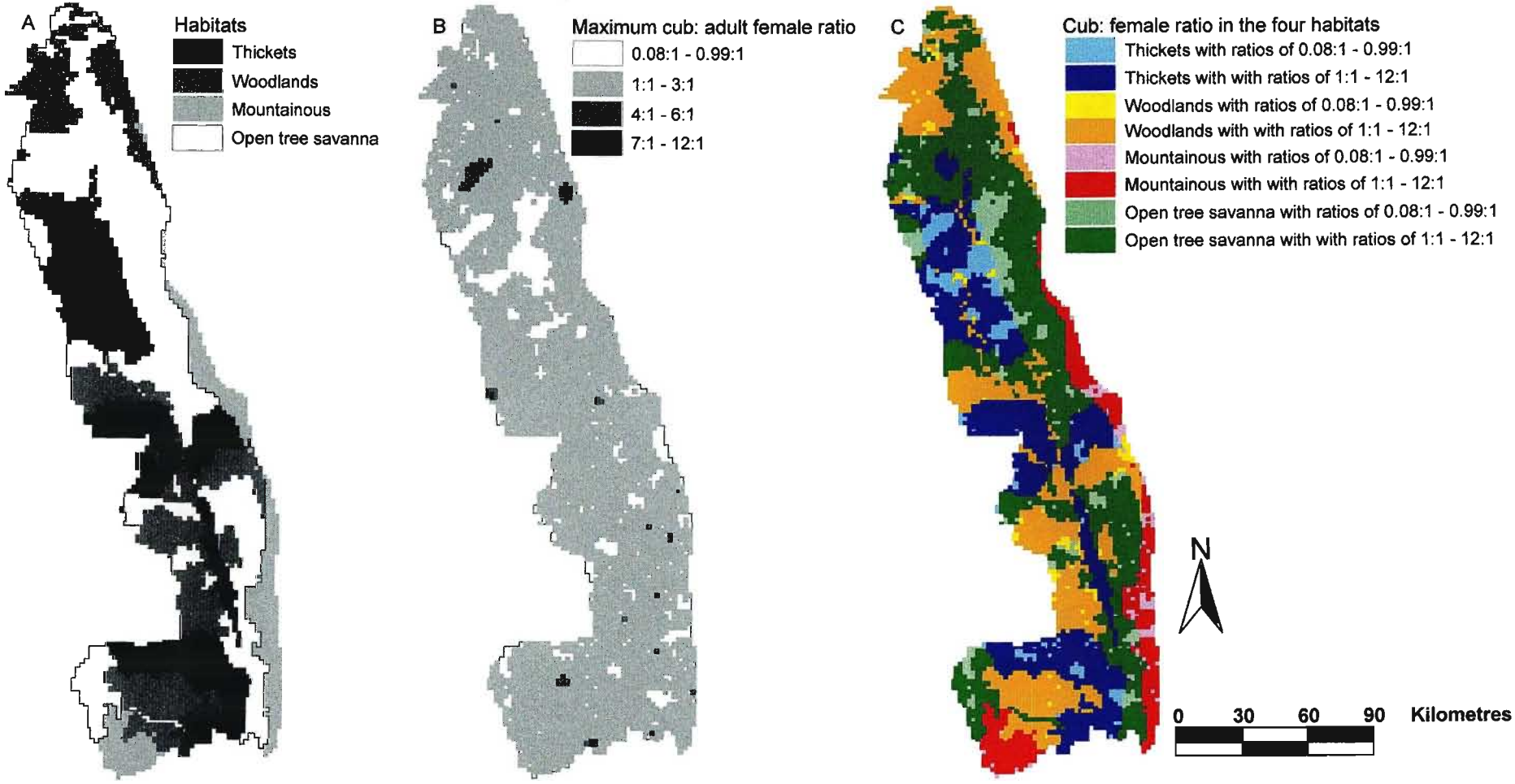

Figure 2.16. The surface map of maximum cub: adult female ratios (B) was overlaid on the habitat map (A) to determine areas of low to high productivity in KNP (C). For ease of interpretation only two ratio categories were used for the map combining habitat and ratio (C). The cub: female ratio was generally greater than one cub per female in all habitat types throughout the park (C). However, there were larger areas of low productivity (less than one cub per female) in thickets and open tree savanna in northern KNP (C). The maps have a grid cell size of one minute².

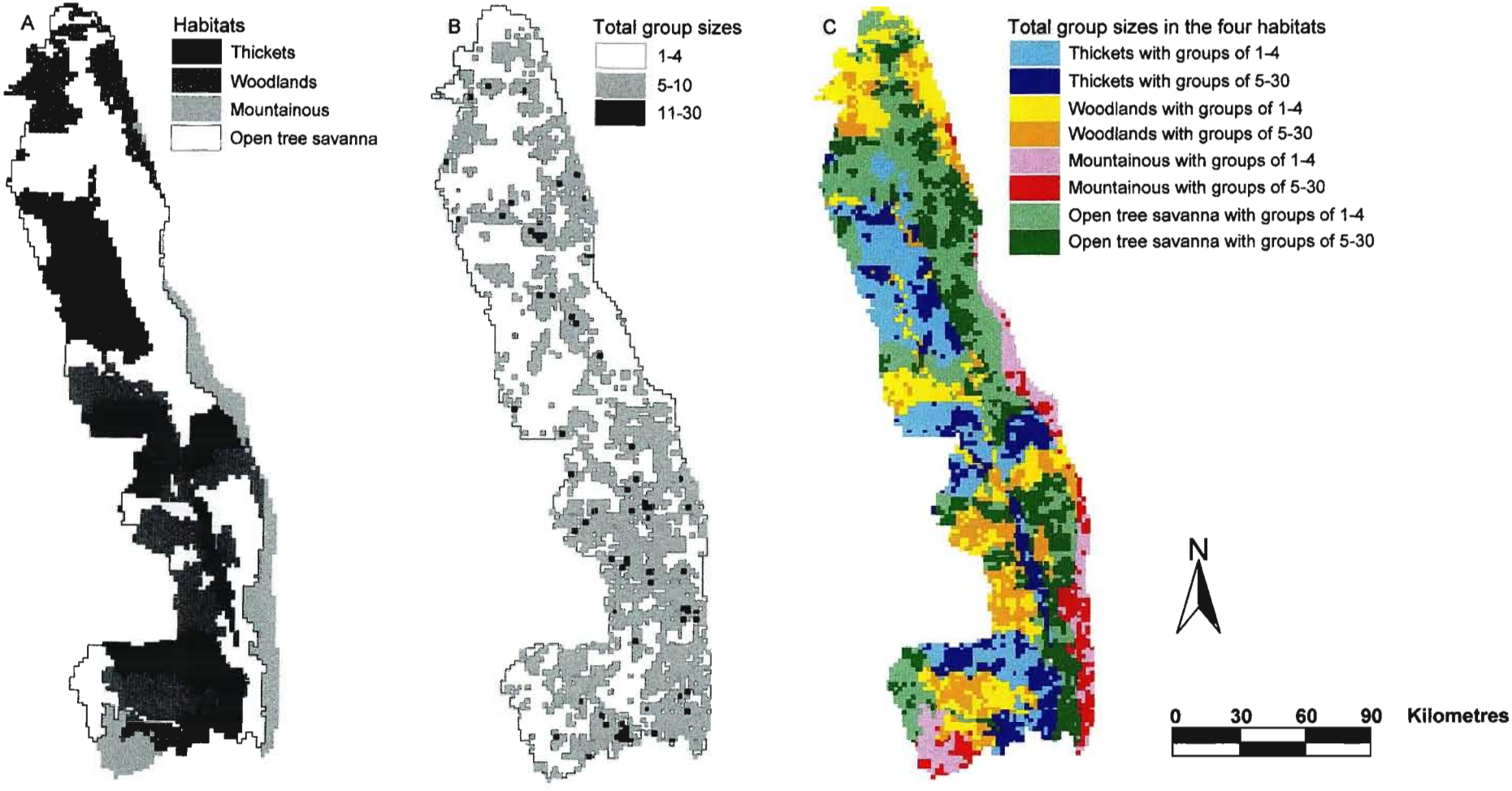

Figure 2.17. The surface map showing the distribution of maximum total lion group sizes (B) was overlaid on the habitat map (A) to determine the spatial distribution of total lion groups through KNP (C). For ease of interpretation only two measures of group size were used for the map combining habitat and group size (C). Larger groups (five to 30) were predominant in the central and southern areas of KNP, while smaller groups predominated in the north, regardless of habitat type (C). The maps have a grid cell size of one minute^2.

Discussion

Habitat selection by an animal is based on many factors related to both the environment and to the interactions between conspecifics and between species (Bond *et al.* 1980; Mills 1982; Rowe-Rowe & Meester 1982; Christensen & Persson 1993; Ritter & Bednekoff 1995; Warrick & Cypher 1998). Animals choose a habitat based on factors such as cover, water availability and the density of competitors and/ or predators, but one of the most important factors is the availability and distribution of food resources (Krebs & Davies 1993). In order for animals to survive and ultimately breed, they require sufficient energy resources. How these resources are distributed, their quantity and quality, can determine where animals choose to settle and for how long (Stephens & Krebs 1986; Krebs & Davies 1993).

Ideal free distribution (IFD) states that animals will settle in the resource-rich habitat first until the benefits gained by settling in the resource-poor habitat are equal to those attained in the resource-rich habitat (Fretwell & Lucas 1970; Regelman 1984). Although one habitat is of lower quality, there will be less interspecific competition (Krebs & Davies 1993). Lions live in fission-fusion groups, the size of which will be influenced by various social and environmental factors (Schaller 1972; Packer *et al.* 1990). Although lion group dynamics have been compared between habitat types, these studies have been based on the prey availability in those areas (e.g. van Orsdol *et al.* 1985; Hanby *et al.* 1995). I compared group sizes of different lion variables across structural habitat types to determine if differences in lion distribution and group size occurred. I predicted that larger groups would be supported in more favourable habitats. Although total group sizes did not differ significantly between habitat types, I found differences in the group sizes when individual lion variables were studied.

Larger coalition sizes are more advantageous as they can potentially hold tenure over a pride for longer than smaller coalitions (Schaller 1972; Bygott *et al.* 1979; Packer & Pusey 1982). One would therefore expect the male coalitions with females to be larger than those without, a result supported by previous studies (but see Stander 1991; Funston & Mills 1997). In this study, the average size of male coalitions both with and without lionesses was similar (median of about 1.5), but the average maximum coalition sizes differed, with male coalitions with females being larger than the average maximums recorded for male coalitions alone. However, as I did not have identification information for the lions, those sightings of coalitions on their own will include males that do hold tenure but are not currently with their pride.

In all four habitats more sightings of males in mixed groups were made than of exclusively male groups. This is either a result of males remaining with their pride almost constantly because their cubs are young or the females are in oestrus, or males alone are more stealthy and remain hidden (Creel & Creel 1997). There is great danger, especially for young male lions, in entering the territory of unknown males. Generally, males will lose the resultant fight if they are still young (or subadults)(Schaller 1972).

I found that the group sizes of females in mixed groups and exclusively female groups did not differ significantly between habitat types, although there were more sightings in the open tree savanna. Wildebeest and zebra, which are species hunted by females, also select more open habitats, which could explain females' preference for the open tree savanna areas (Funston *et al.* 1998).

While my data produced a sex ratio in favour of females (44 to 47% males), which is in agreement with studies done elsewhere, the ratio was not significantly different from a 50:50 ratio (Central district of KNP – 29 to 37% males, Smuts 1976; Etosha National Park - ± 38% males, van Orsdol 1984; Selous Game Reserve – 36 to 41% males, Creel & Creel 1997). In the studies mentioned above, the authors had identification information and were therefore able to calculate the sex ratio more accurately. My results are based on per-cell calculations without the advantage of identification information, which reduces the accuracy of the actual value of the ratio calculated.

Although there were more sightings than expected of subadults and cubs in the open tree savanna, both subadult and cub group sizes were larger in the woodlands. The woodlands provide protected areas for cubs while still providing a good environment for hunting, while the open tree savanna has fewer hidden areas but still provides good visibility of the surrounding area and cover for hunting. Food supply has been found to affect cub survival (Bertram 1973) in the Serengeti, therefore lions with cubs may choose the habitats with greatest food abundance. The relationship between cub distribution and group sizes compared to prey abundance is investigated further in Chapter Three. There was little difference between the total group sizes recorded in the four habitats, with all four habitats having a median average group size of about four. However, in a study comparing prides in the Serengeti plains and the Ngorongoro crater, despite differences in prey availability, there were no differences between the pride sizes recorded (Hanby *et al.* 1995).

The number of sightings per habitat type for each lion variable differed, but all showed a general preference for the open tree savanna and/ or thickets. This result is supported by the findings of Mills & Biggs (1993) and Mills & Gorman (1997) for lions in KNP. Although the mountainous areas appeared to be important this may have been an artefact of data collection rather than a true pattern of habitat preference. As stated in the results, the importance of mountainous areas may be overestimated as a result of these areas lying along the park boundaries and therefore receiving more attention than central areas.

Lions will select habitats based on factors such as prey availability, cover for hunting and protection for cubs. The comparison of prides between the Ngorongoro Crater and the Serengeti plains, showed that while prey availability was greater in the Crater, there was higher conspecific aggression and conflicts, which resulted in lions moving on to the plains where prey is more variable (Hanby *et al.* 1995). This would support the concept of IFD which suggests that after a certain point, it is better to settle in the poorer habitat as competition for resources will be lower (Krebs & Davies 1993). In terms of group size, while some studies have found that larger groups form where prey is scarce (Stander 1992b), there is also support for the IFD assumption that more individuals can settle in the resource-rich area (e.g. van Orsdol 1982). In this study, lions mainly selected the open tree savanna habitats, which are also the areas preferred by their favoured prey species; a result that supports the concept of IFD. However, in terms of lion group size there are other social factors, including cub and territory defence, that should be taken into account as they are often more influential than food availability (Packer *et al.* 1990). Although IFD and other foraging models are useful tools for explaining habitat selection by animals, they cannot always account for group distribution, as it is not only food availability that influences habitat selection (e.g. Bond *et al.* 1980; Mills 1982; Ritter & Bednekoff 1995; WallisDe Vries 1996; Perrin & Everett 1999).

In conclusion, my study has shown that lions select for particular habitat structures (open tree savanna and thickets) that confer advantages in terms of hunting, cover for cubs and visibility of surrounding areas. However, while individual lion variable group sizes may differ between habitat types, there is no difference between the total group sizes or female group sizes observed in all habitat types.

CHAPTER THREE
THE EFFECT OF PREY ABUNDANCE AND DISTRIBUTION ON LION GROUP DYNAMICS

Introduction

Distribution and availability of food resources is an important factor in determining the distribution and density of animals (Melton 1987; WallisDe Vries 1996). The distribution of predators is related to the distribution of their prey species (Mills 1982; East 1984; Creel & Macdonald 1995; Funston *et al.* 1998; Andreka, Linn, Perrin & Maddock 1999), which is itself determined by the quantity and quality of forage and browse available and in water-dependent species, on the distribution of water sources (Western 1975; Ritter & Bednekoff 1995; Owen-Smith 1996). Natural populations of large herbivorous savanna mammals tend to be close to the limits that are set by their food resources (East 1984).

Prey distribution not only affects predator distribution, but together with prey abundance can also influence predator group formation, group size and territory size (Macdonald 1983). As discussed in Chapter One, the resource dispersion hypothesis (RDH) states that group size is determined by patch quality while territory size depends on patch distribution (Meia & Weber 1996). Lions hold territories where the availability of food, water and the presence of other prides determines the territory size (Orford 1986; Stander 1991). However, these vary very little over the long-term (Bertram 1973).

Lions live in fission-fusion groups (Schaller 1972; Packer *et al.* 1990) that result from a variety of factors such as protecting their young and maintaining a long-term territory (Packer *et al.* 1990). However, factors such as prey distribution and availability may also influence group size. While a prey-rich patch can support a larger group, forming a larger group in a prey scarce area can also increase an individual's probability of fulfilling its minimum daily food requirements (Stander 1992a). Where prey are abundant, individuals in all group sizes should attain or exceed their minimum daily food requirements (Packer *et al.* 1990; Stander 1992a).

Food resources and water limit prey abundance, not only on a spatial scale, but also seasonally (Holekamp, Smale, Berg & Cooper 1997). Herbivores gather where their preferred food is and those that are water-dependent will remain within a certain distance of water (Western 1975; Hunter 1996). In Kruger National Park (KNP), during summer, food should be more influential as there is normally sufficient surface water from the rains. During winter, the dry months,

water-dependent herbivores will be more dependent on the numerous watering points in the park. However, the vegetation in the immediate vicinity of the waterholes is soon depleted by the presence of numerous browsers and grazers (Mills & Retief 1984; Kalikawa 1990). The animals have to move further away from the watering points in order to gain sufficient food. Thus, in winter, the herbivores will break up into smaller groups, which may influence the group size formed by a social predator such as the lion.

While prey abundance may influence predator group size, the actual body size/ mass of the prey individuals can affect predator group sizes through its influence on hunting success (Cooper 1990). Spotted hyaenas (*Crocuta crocuta*) in the Serengeti had greater success hunting larger prey items when they were in big groups (Kruuk 1972). The hunting success rate of lions in the Queen Elizabeth National Park, Uganda, increased with the number of lions participating in the hunt (Van Orsdol 1984). Although larger groups are also better able to defend their prey from other predators, there is more intra-group competition for the carcass (Carbone, du Toit & Gordon 1997).

Seasonal changes in prey availability brought about by a decrease or moving away by main prey species, can result in a change in the food habits of predators (Amerasinghe, Ekanayake & Burge 1990; Cooper 1990; Seip 1992). However, the vulnerability of prey is important to predators (Bertram 1973; Iriarte, Franklin, Johnson & Redford 1990; Mills *et al.* 1995). Although there may be a high abundance of a certain prey species in an area, if the animal is difficult to catch, it is not advantageous for the predators to remain in the area. In the Serengeti, lionesses have been known to move 20 to 40 km from their usual territories to reach the migratory herds (Packer *et al.* 1990). Cheetah (*Acinonyx jubatus*) will also follow their prey when it moves in the drier months, even if it means moving out of their own territory (Caro 1994).

Although lions are not known to be seasonal breeders (Schaller 1972), the lions in central KNP were observed to produce cubs during the period when their major prey species produced their young (Smuts *et al.* 1978). In the Serengeti, the females were most often in oestrus during seasons of prey abundance (Packer *et al.* 1990). Cub survival depends mainly on nutrition, therefore prey distribution and vulnerability is important to maternal females (Van Orsdol *et al.* 1985; Sunquist & Sunquist 1989).

Prey are an important biotic mechanism driving the dynamics of group formation in social animals. There are two mechanisms by which prey can affect predator dynamics, firstly prey abundance (biomass) and secondly, prey type selection can influence group formation. In terms of prey abundance, the resource dispersion hypothesis (RDH) states that group size is determined by the quality or richness of the resource patches in the area while territory size is determined by the distribution of the resource patches (Macdonald 1983; Meia & Weber 1996). It predicts that group size will be largest in areas of high prey abundance and that territory size will be greatest where patches are widely distributed (Macdonald 1983). Due to the limitations of my data, I did not study the effect of patch distribution on territory size, only the effects of patch richness on group size. I decided to work with seven of the larger lion prey species, including buffalo, giraffe, impala, kudu, waterbuck, wildebeest and zebra. Smaller kills are often missed (completely devoured) which could lead to underestimates and wrong conclusions about the importance of these animals in the lions' diet (Pienaar 1969; Ruggiero 1991). I used two measures of prey availability to test the hypothesis, firstly, the biomass of the seven prey species available (including and excluding buffalo biomass) and secondly, the actual abundance of each of the seven prey species. I predicted that larger lion groups would occur in areas of greatest prey availability and that cub presence, cub group sizes and reproductive output would be greater in areas of higher prey abundance.

Prey selection may be governed by a number of factors, including the size of the prey species, it's condition, their relative abundance in the total prey base and the size and composition of the foraging group (Kruuk 1972; Schaller 1972; Packer 1986; Packer & Ruttan 1988). My aim for this section was to describe lion prey selection based on prey size and availability. Previous studies have found that larger hunting groups have greater success hunting larger prey items than smaller groups (Kruuk 1972; Packer & Ruttan 1988). As a result, I expected larger groups of lions to be present at kills of larger prey species. In terms of group composition, previous studies have shown a strong correlation between male lions and impala and buffalo kills (Funston *et al.* 1998), while impala, zebra and wildebeest are important to females (Rudnai 1974; Scheel 1993; Funston *et al.* 1998). I only compared male and female presence at buffalo and wildebeest kills, expecting male lions to be present more often at buffalo kills and, females to be present more often at wildebeest kills. Following this, I also expected group composition to vary with prey species composition, where composition referred to the proportion that each of the seven prey species contributed to the total number of individuals present. I also looked at the distribution of kills relative to the actual abundance (number of individuals) of each species, to determine if lions were selecting for specific species regardless of whether the species was in

high or low abundance relative to its (the prey species') spatial distribution.

Methods

Prey data

Aerial census counts of certain prey species in KNP are usually carried out between May and August, the drier period of the year. I worked with the aerial census data from 1978 until 1985. Although census counts were carried out prior to 1978, I only used the data from 1978 as this corresponds to the first year when full aerial censuses were carried out. I did not use data beyond 1985, as this was the year when the monthly predator returns were stopped. The census databases for each year contain the species name, number counted, year, census area, and latitude and longitude locations of the animals counted. I extracted the data for the following major prey species: buffalo, giraffe, impala, kudu, waterbuck, wildebeest and zebra. The data for each species are summarised in the form of line graphs showing the total population fluctuations from 1978 to 1985 (Appendix 3.1).

I used the aerial census data to create annual maps detailing the actual number of each prey species counted that year (Appendix 3.2). These maps had the same dimensions and cell sizes as the habitat map of Chapter Two and the lion variable maps. I created surface distribution maps for each prey species for each year, which I then averaged, for each species over the eight-year period, resulting in seven surface distribution (abundance) maps, one per species (Appendix 3.3).

Lion variables

I used the lion observation data from the ranger diaries and monthly predator returns for the three-month period from July to September as this corresponds to the dry period when the aerial censuses are carried out. I used the data from the years 1978 to 1985. Details of the lion data are presented in Chapter One.

The average and maximum values were calculated per grid cell for the following lion variables resulting in two maps for each variable for each year except number four (only one map):

1. adult males in:
   1.1. mixed groups
   1.2. exclusively adult male groups
2. adult females in:
   2.1. mixed groups
   2.2. exclusively adult female groups

3. cubs
4. cub to adult female ratio
5. subadults
6. total group size

The eight average maps for each variable, eight maximum maps for each variable and one ratio map for variable four were separately added and averaged over the eight-year period. This resulted in the generation of 15 final lion variable maps that had averaged average, averaged maximum or averaged ratio values for each cell. Hereafter I refer to the averaged average and averaged maximum groups sizes as the average and maximum, respectively.

Resource dispersion

I used two methods to test if the RDH could be used to explain why lions form larger groups in certain areas and smaller groups in others. Firstly, I used total prey biomass availability and secondly, actual individual species abundance, as measures of prey abundance.

In terms of biomass as a measure of prey availability, I created two biomass maps; one including and one excluding buffalo biomass. Using the masses as listed by Mills & Hes (1997), I averaged the adult male and adult female masses for each of the seven species to obtain an average mass for each species. I then multiplied the averaged surface maps (i.e. average abundance over eight years) for each species by the average mass for that species (Table 3.1) to create the seven prey biomass availability maps, one per species.

Table 3.1. I used the average of the adult male and adult female biomasses for each species to create the prey biomass maps (Biomass values from Mills & Hes 1997).

Prey species	Mass (kg)
Buffalo	750
Giraffe	1010
Impala	50
Kudu	255
Waterbuck	260
Wildebeest	215
Zebra	310

I added the prey biomass maps to create one map of total prey biomass (Fig. 3.1A) and a second that excluded the buffalo biomass (Fig. 3.1B). The biomass categories created for the two final maps differed in size as the contribution of buffalo mass to the total prey biomass in each cell was large (Fig. 3.1). I used different size categories for the two maps as the exclusion of buffalo

mass resulted in biomass values that only fell into the first two categories used for the total biomass map.

Using the grid cell references based on the index map (see Chapter One for details), I extracted the data from the two biomass category maps and the 15 lion variable maps into a database. As the data were not normally distributed (Kolmogorov-Smirnov, $P < 0.05$), I used Kruskal-Wallis one-way ANOVA to compare the 15 lion variables in each biomass category for both the total and total less buffalo biomass categories (Zar 1999). The test variables were one of 15 dependent variables and the grouping variable was category type (minimum = 1, maximum = 6 for total, see Fig. 3.1A legend; minimum = 1, maximum = 4 for total less buffalo, see Fig. 3.1B legend). I applied the Bonferroni adjustment to the significance levels used for each variable because the same data were used for multiple tests (Table 3.2; Schork & Remington 2000). The pattern for the average and maximum variables was similar, so only the maximum lion variable data are illustrated using box-and-whisker plots showing the median, first and third quartiles and the range. Although, outliers and extremes were used in the analyses I have not represented them in the box plots in order to avoid cluttering and to facilitate interpretation of trends.

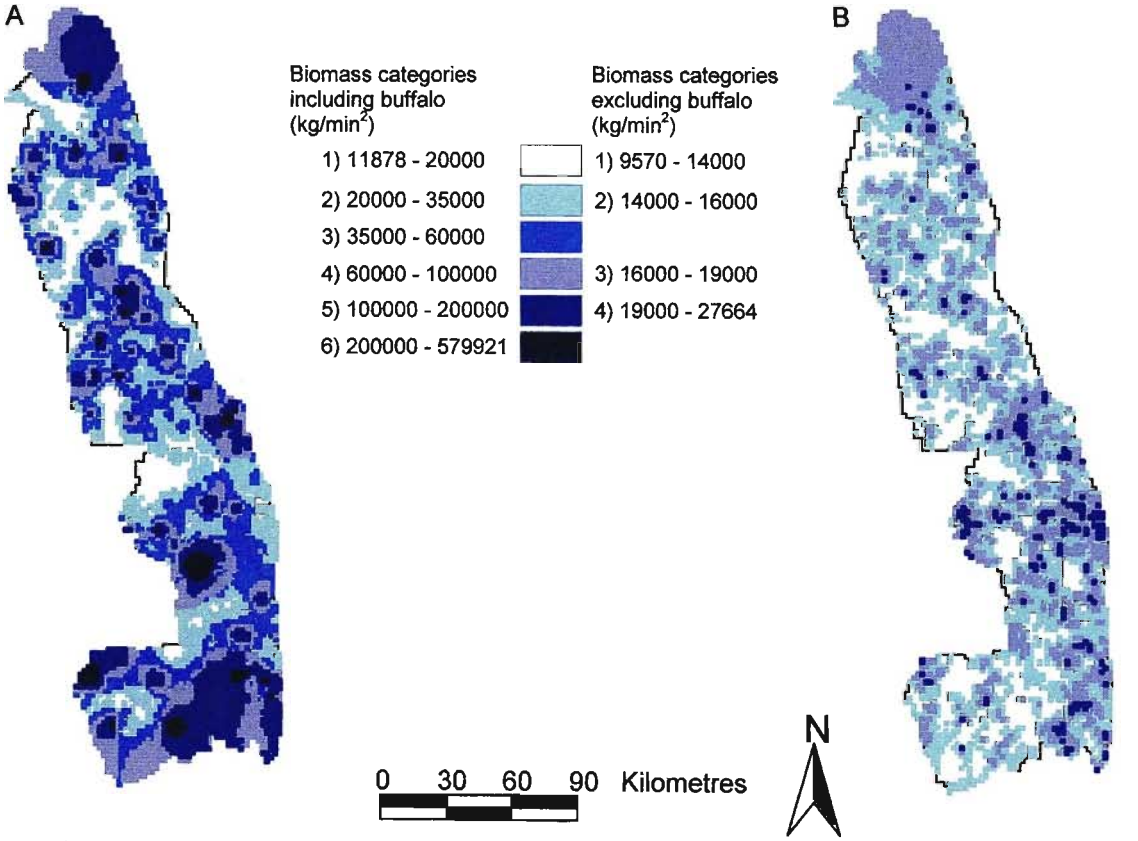

Figure 3.1. Prey biomass maps showing spatial variability in the mass of prey available in KNP, (A) including and (B) excluding buffalo biomass. The maps have a grid cell size of one minute². Note that the legend scales differ for the two maps, i.e. the colour categories are not equivalent.

My second test of the RDH was based on individual prey species abundance, and each species' influence on lion group size. I extracted the data from each prey species surface map and all average, maximum and ratio lion variable maps into a database. As the data were not normally distributed (Kolmogorov-Smirnov, $P < 0.05$), I ran a Spearman correlation analysis to determine if any correlations existed between the abundance of each of the seven prey species and the 15 lion variables as listed above (Zar 1999). I applied the Bonferroni adjustment to the significance levels used for each variable because the same data were used for multiple tests (Table 3.2; Schork & Remington 2000). For each variable I calculated the critical P-value as 0.05 divided by the number of tests that that variable and related variables had been used for.

Table 3.2. I adjusted the significance levels for the lion variables used in all analyses mentioned above based on the number of tests that each variable was used in or not independent of for each separate analysis. The adjusted value was calculated as P = 0.05 divided by the number of tests.

Variable	Tests	Number of tests	P [a]
Adult male group sizes	Average and maximum adult males in mixed groups, average and maximum exclusively adult male group sizes, average and maximum total group sizes	6	0.008
Adult female group sizes	Average and maximum adult females in mixed groups, average and maximum exclusively adult female group sizes, cub: adult female ratio, average and maximum total group sizes	7	0.007
Subadult group sizes	Average and maximum subadult group sizes, average and maximum total group sizes	4	0.013
Cub group sizes	Average and maximum cub group sizes, cub: adult female ratio, average and maximum total group sizes	5	0.01
Cub: adult female ratio	Average and maximum adult females in mixed groups, average and maximum exclusively adult females, average and maximum cub group sizes, cub: adult female ratio, average and maximum total group	9	0.006
Total group sizes	All the above mentioned variables	15	0.003

[a] P = Bonferroni adjusted critical P level for significance testing (Schork & Remington 2000).

I illustrated the significant results only by comparing the lion variable surface maps with the surface maps of prey abundance.

Prey selection

In order to formulate a description of prey selection by lions in KNP, I looked at the lion group size and composition at the kills of seven prey species (buffalo, giraffe, impala, kudu, waterbuck, wildebeest and zebra), the spatial distribution of kills as well as the spatial prey base composition. I obtained kill data from the ranger diaries and monthly predator returns. I also used the lion variables and the prey surface abundance maps as calculated above for part of the analyses.

As an overview to the kill data, I have listed all the species reported to be killed by lions, calculated the proportion (number and biomass) of each species in the diet and plotted these data over time. I used the species biomasses listed in Mills & Hes (1997). When the sex of the kill was not given, I used the average of the adult male and adult female biomasses. When the carcass was described as juvenile, I used half the mass of an adult female, with the exception of the elephant calves for which I used the mass at birth of 100kg. I assumed that the lions had made the kill and excluded those data where it specified that the carcass had been scavenged from another predator or had died from other causes. Although these data were limited, it should reflect any patterns or trends in the species killed. However, smaller species may be under-represented, as the carcasses are often not found as they are completely consumed.

To determine if group size and composition varied between kills, I drew up a table detailing the total number of males, females, subadults, cubs and total group size at each kill. As the data were not normally distributed (Kolmogorov-Smirnov, $P < 0.05$), I used Kruskal-Wallis one way ANOVA to compare the lion variable group sizes at the kills of the seven species (Zar 1999). I applied the Bonferroni adjustment to the significance levels used for each variable because the same data were used for multiple tests (Schork & Remington 2000). For each variable I calculated the P value as 0.05 divided by the number of tests that that variable and related variables had been used for. Thus for these analyses, the critical P-values used for adult males, females, subadults and cubs was $P = 0.025$ (0.05/2) while that for total group size was 0.01 (0.05/5). I divided by two for the individual lion variables, as these were not independent of the total group size. I divided by five for the total group size, as the data used for this test was not independent of any of the individual lion data. Box-and-whisker plots showing the median, first and third quartiles and the range are used to illustrate the data. Although, outliers and extremes were used in the analyses I have not represented them in the box plots in order to avoid cluttering and to facilitate interpretation of trends.

Buffalo are an important prey species of male lions, while wildebeest are important to adult females (Rudnai 1974; Scheel 1993; Funston *et al.* 1998). To determine if the presence of adult males and females differed at the kills of buffalo and wildebeest, I drew up a contingency table of the total observations of males only, females only and males with females present at the kills of buffalo and wildebeest. I used a G test to test for significant differences between the two prey species (Zar 1999). As the data for males only and females only is not independent of that for males with females, I adjusted the significance level of the test by dividing the significance level of $P = 0.05$ by two to obtain a new critical level of $P = 0.025$ (Bonferroni adjustment, Schork &

Remington 2000). I have illustrated the result with a bar graph showing the number of observations of males only, females only and males with females present at buffalo and wildebeest kills.

To determine if lion group composition and size varied with the spatial prey species composition, I compared the lion variables against the proportion of specific prey species comprising the total prey base. I used the database created in the previous section that contained the lion variables and the values of prey species abundance in each grid cell (one minute^2) of KNP. I calculated the proportion (in terms of number of individuals) that each prey species contributed to the total number of prey individuals in each grid cell. As the data were not normally distributed (Kolmogorov-Smirnov, $P < 0.05$), I ran a Spearman correlation analysis to compare the proportion of each prey species in the total prey composition and the lion variables, as listed above, in each cell (Zar 1999). I only used the averaged average lion variables and the cub: adult female ratio for this analysis as the large number of tests on these data decreases the power of the analysis because of the Bonferroni adjustment. I adjusted the significance levels used for each lion variable by dividing the P value of 0.05 by the number of tests that that variable and related variables had been used for (Table 3.3; Schork & Remington 2000).

Table 3.3. I adjusted the significance levels for the Spearman correlation analyses relating the lion variables to prey species availability based on the number of tests that each variable was used in or not independent of for each separate analysis. The adjusted value was calculated as P = 0.05 divided by the number of tests.

Variable	Tests	Number of tests	P [a]
Adult male group sizes	Average adult males in mixed groups, average exclusively adult male group sizes, average total group sizes	3	0.017
Adult female group sizes	Average adult females in mixed groups, average exclusively adult female group sizes, cub: adult female ratio, average total group sizes	4	0.013
Subadult group sizes	Average and maximum subadult group sizes, average and maximum total group sizes	2	0.025
Cub group sizes	Average cub group sizes, cub: adult female ratio, average total group sizes	3	0.017
Cub: adult female ratio	Average adult females in mixed groups, average exclusively adult females, average cub group sizes, cub: adult female ratio, average total group	5	0.01
Total group sizes	All the above mentioned variables	8	0.006

[a] P = Bonferroni adjusted critical P level for significance testing (Schork & Remington 2000).

Kill distribution versus prey abundance

I created kills surface maps for each of the seven prey species using data from 1957 to 1988 (Appendix 3.4). I created abundance proportions maps for each species using the prey census

surface maps by normalising the data, i.e. all cells had values from zero to one. I did this by dividing each abundance map by the maximum number of individuals recorded in any cell for that species. I also normalised the kill surface maps for each species by dividing the kill maps by the maximum number of kills recorded in a cell for that species. I divided both sets of proportions data into 10 equal continuous categories. I compared the distribution of frequencies for the kill and abundance proportion data using a Kolmogorov-Smirnov goodness-of-fit test (Zar 1999). The results are illustrated by seven maps showing the difference between the two proportions maps for each species (abundance proportions map subtracted from kill proportions map).

Results

Effect of resource dispersion

Adult males in mixed groups

There were no significant differences between the group sizes of adult males in mixed groups recorded in the prey biomass categories of either total prey biomass or total less buffalo biomass (Tables 3.4 & 3.5 and Figs 3.2 & 3.3, respectively). The distribution of adult male lions in mixed groups will be driven by their association with females, especially that of mating males. Therefore prey biomass availability and distribution may not influence coalition size.

Significant positive correlations exist between impala abundance and the average and maximum group size of adult males in mixed groups (Table 3.6; Fig. 3.4). Adult male group size therefore increased with an increase in impala abundance. There were positive correlations between wildebeest abundance and the average and maximum group size of adult males in mixed groups, but these were not significant relationships (Table 3.6). Impala are an important prey species of adult males (Funston *et al.* 1998) which may explain their increasing group size where these prey are in abundance. Males may be forming/ remaining in larger groups where these prey are more abundant because of an increased presence of females.

Exclusively adult male groups

Neither the average nor maximum group sizes differed significantly between the biomass categories based on total prey biomass only or when buffalo biomass was excluded (Tables 3.4 & 3.5, Figs 3.2 & 3.3, respectively). The biomass of the species available may be less important than the actual prey base species composition.

There were positive correlations between buffalo abundance and both average and maximum exclusively adult male group size, however, only the correlation with average group size was significant (Table 3.6). Average male coalition sizes were significantly higher in the areas of higher buffalo abundance and significantly lowest in areas of low buffalo abundance (Fig. 3.5). Adult males are important in the hunting of larger prey species (Packer 1986). Therefore coalition members may be staying together or forming larger groups where buffalo are in abundance because of an increased hunting success with an increase in group size.

Adult females in mixed groups

There were no significant differences between the adult female group sizes based on the total prey biomass categories or the biomass categories when buffalo were excluded (Tables 3.4 &

3.5, Figs 3.2 & 3.3, respectively). The biomass of prey available may not be as influential in determining group size as the actual species available themselves.

Both the average and maximum group sizes of adult females in mixed groups were positively correlated with impala abundance, although these correlations were not significant because of the adjusted significance levels (Table 3.6).

Exclusively adult female groups

Based on biomass availability, there were no significant differences between group sizes based on either total prey biomass or total prey less buffalo biomass (Tables 3.4 & 3.5, Figs 3.2 & 3.3, respectively). As I mentioned for adult females in mixed groups, there may be factors other than biomass affecting exclusively adult female group size such as the vulnerability of the prey available.

Although there were positive correlations between buffalo abundance and both the average and maximum exclusively adult female group size, neither of these correlations were significant (Table 3.6).

Subadults

There were no significant differences between the subadult group sizes in the biomass categories based on either measure of prey biomass availability (Tables 3.4 & 3.5, Figs 3.2 & 3.3, respectively). Subadult group size was also not correlated with the abundance of any of the seven prey species. Although lions can hunt from the age of two (Schaller 1972), their distribution will be influenced by that of their mothers. Funston, Mills & van Jaarsveld (in prep.) suggested that the distribution of subadult males evicted from prides in southern KNP was influenced to a large extent by buffalo distribution as these are important prey of male lions (Funston *et al.* 1998). However, there may also be other factors affecting their distribution once evicted from the pride, such as the distribution of other male coalitions.

Cubs

Cub group size did not differ significantly between the biomass categories based on either total biomass or when buffalo biomass was excluded (Tables 3.4 & 3.5, Figs 3.2 & 3.3, respectively). Nor was cub group size correlated with the abundance of any of the seven prey species. Cub survival and hence, group size, is strongly influenced by nutrition (Van Orsdol *et al.* 1985).

Therefore the vulnerability of the prey available may be more important than their abundance when cubs are present in a pride.

Cub: adult female ratio

There were no significant differences between the cub to adult female ratio in either the total prey biomass categories or between the biomass categories when buffalo biomass was excluded (Tables 3.4 & 3.5, Figs 3.2 & 3.3, respectively). The correlation between the cub to adult female ratio and zebra abundance was negative, but not significant (Table 3.6). Nutrition is very important to cub survival after birth (Van Orsdol *et al.* 1985). However, it is not only the abundance of prey species (numbers and biomass) that will affect cub survival but the mothers' ability to catch prey. Therefore the vulnerability of the prey available may also affect cub survival and reproductive output.

Total group size

Total group size was not significantly different between the total prey biomass categories or the categories when buffalo biomass was excluded (Tables 3.4 & 3.5, Figs 3.2 & 3.3, respectively). Average and maximum total group sizes were correlated with both impala and kudu abundance (Table 3.6). However, the correlation with impala was positive and significant for maximum group size, while the correlation with kudu was negative with neither correlation significant. Total lion group sizes therefore increased with an increase in impala abundance (Fig. 3.6). Impala are an important prey species for both males and females (Funston *et al.* 1998) which may explain the increase in total group size with increasing impala abundance.

Table 3.4. Prey abundance, or patch richness, will influence group formation and size in social predators. Using biomass as a measure of patch richness, I compared lion group sizes in six biomass categories (see legend of Fig. 3.1) using Kruskal-Wallis one-way ANOVA.

Lion variables		Average group size		Maximum group size		Ratio	
	N [1]	χ^2	P	χ^2	P	χ^2	P
Adult males in mixed groups [a]	398	5.955	ns	7.653	ns		
Exclusively adult males [a]	276	13.711	0.018	12.534	0.028		
Adult females in mixed groups [b]	417	4.592	ns	4.716	ns		
Exclusively adult females [b]	106	6.993	ns	7.372	ns		
Subadults [c]	114	1.635	ns	1.615	ns		
Cubs [d]	97	7.082	ns	6.919	ns		
Cub: adult female [e]	95					1.397	ns
Total group [f]	630	7.738	ns	7.213	ns		

Df = 5 in all cases.
[1] N = sample size
Note: The critical significance levels have been adjusted as the data were used in multiple tests (Schork & Remington 2000). The adjusted critical P values are: [a] P = 0.008; [b] P = 0.007; [c] P = 0.013; [d] P = 0.01; [e] P = 0.006; [f] P = 0.003
Results where P >0.1 have been noted as ns (non-significant), although only results with P< critical level have been interpreted as significant.

Table 3.5. As buffalo are heavy animals, I excluded buffalo biomass in order to test if the biomass of the remaining six prey species influenced group formation and size. I used Kruskal-Wallis one-way ANOVA to compare various lion variables in four biomass categories (see legend of Fig. 3.1).

Lion variables		Average group size		Maximum group size		Ratio	
	N[1]	χ^2	P	χ^2	P	χ^2	P
Adult males in mixed groups [a]	398	5.1773	ns	4.489	ns		
Exclusively adult males [a]	276	1.1825	ns	1.43	ns		
Adult females in mixed groups [b]	417	2.9977	ns	2.228	ns		
Exclusively adult females [b]	106	2.0044	ns	2.174	ns		
Subadults [c]	114	1.3293	ns	1.279	ns		
Cubs [d]	97	1.9337	ns	1.855	ns		
Cub: adult female [e]	95					2.816	ns
Total group [f]	630	5.6302	ns	5.304	ns		

Df = 3 in all cases.
[1] N = sample size
Note: The critical significance levels have been adjusted as the data were used in multiple tests (Schork & Remington 2000). The adjusted critical P values are: [a] P = 0.008; [b] P = 0.007; [c] P = 0.013; [d] P = 0.01; [e] P = 0.006; [f] P = 0.003
Results where P >0.1 have been noted as ns (non-significant), although only results with P< critical level have been interpreted as significant.

Table 3.6. Lion group dynamics are affected by the distribution and abundance of their prey species. I tested for correlations between various lion variables and the abundance of seven prey species using Spearman correlation analysis. Only those prey species and lion variables for which at least one significant result was obtained have been included in the table. Results for which $P \geq 0.1$ have been excluded.

Lion variables			Buffalo		Impala		Kudu		Wildebeest		Zebra	
		N [1]	r_s [2]	P	r_s	P	r_s	P	r_s	P	r_s	P
Adult males in mixed groups	average [a]	398			0.174	0.001			0.11	0.029		
	maximum [a]	398			0.192	<0.001			0.1	0.047		
Exclusively adult males	average [a]	276	0.167	0.005								
	maximum [a]	276	0.154	0.011								
Adult females in mixed groups	average [b]	417			0.111	0.024						
	maximum [b]	417			0.125	0.01						
Exclusively adult females	average [b]	106	0.167	0.088								
	maximum b	106	0.163	0.094								
Cub: adult female	ratio [c]	95									-0.212	0.04
Total group	average [d]	630			0.094	0.019	-0.072	0.072				
	maximum [d]	630			0.115	0.004	-0.082	0.039				

[1] N = sample size

[2] r_s = Spearman's correlation coefficient

Note: The critical significance levels have been adjusted as the data were used in multiple tests (Schork & Remington 2000). The adjusted critical P values are: [a] P = 0.008; [b] P = 0.007; [c] P = 0.006; [d] P = 0.003 Results for which $P \geq 0.1$ have been excluded, although only results with P < critical level have been interpreted as significant.

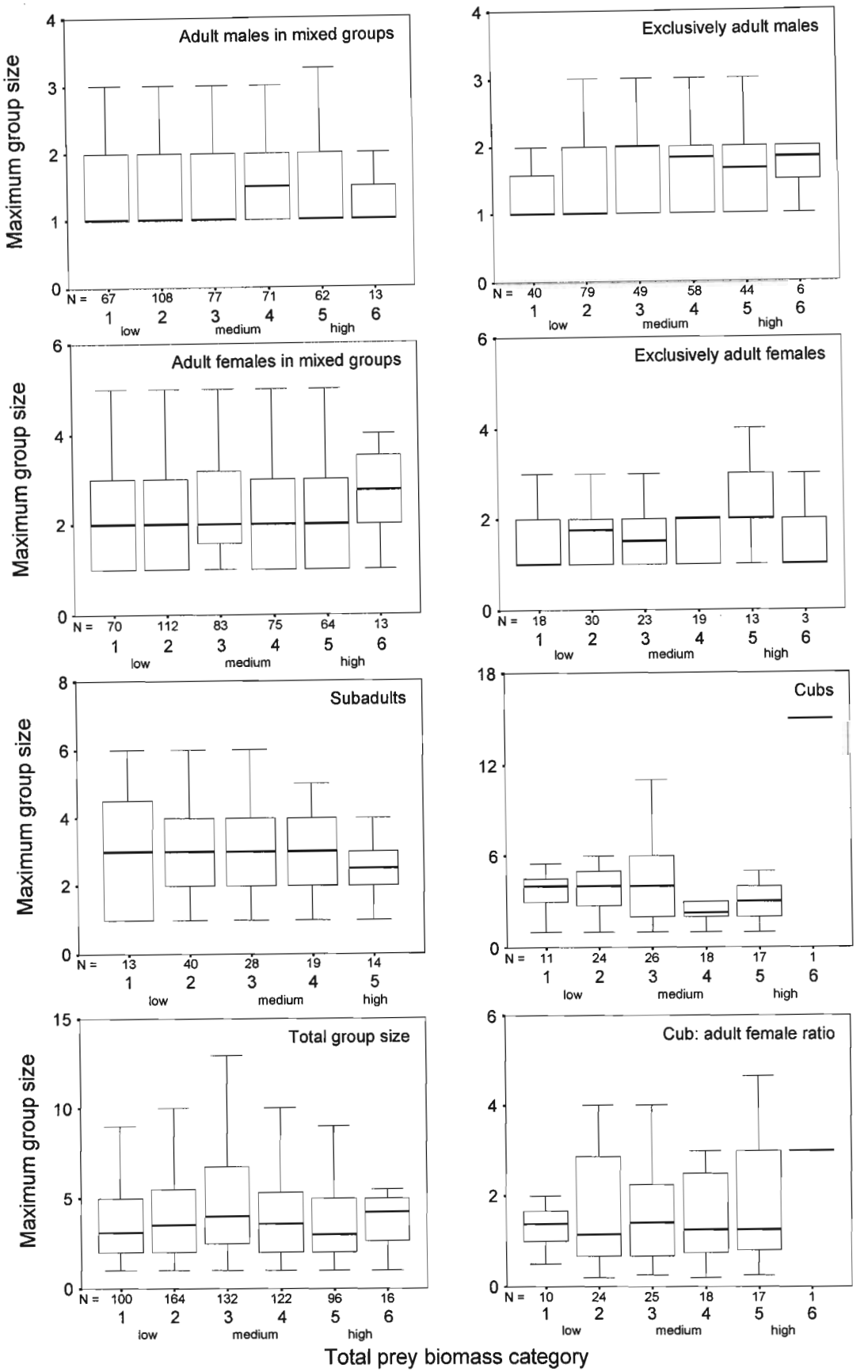

Figure 3.2. Lion group size was not significantly affected by the total biomass of prey available, with the exception of exclusively adult male groups. The box plots show the median, the first and third quartiles and the range of the data, excluding extremes and outliers. Biomass categories are defined in Fig. 3.1. N = the number of cells with data.

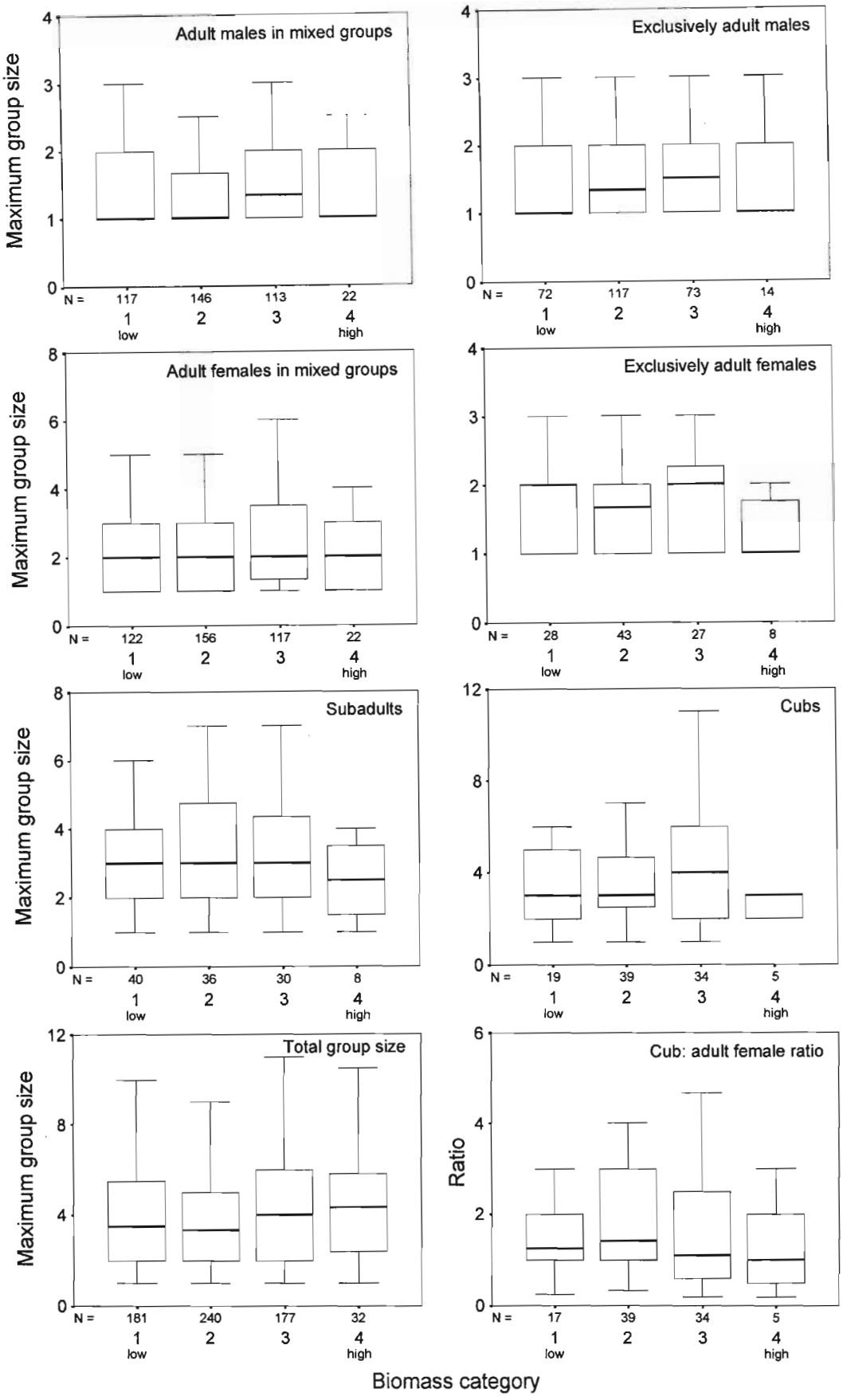

Figure 3.3. Lion group size did not vary between biomass categories when buffalo mass was excluded. The box plots show the median, the first and third quartiles and the range of the data, excluding extremes and outliers. Biomass categories are defined in Fig. 3.1. N = the number of cells with data.

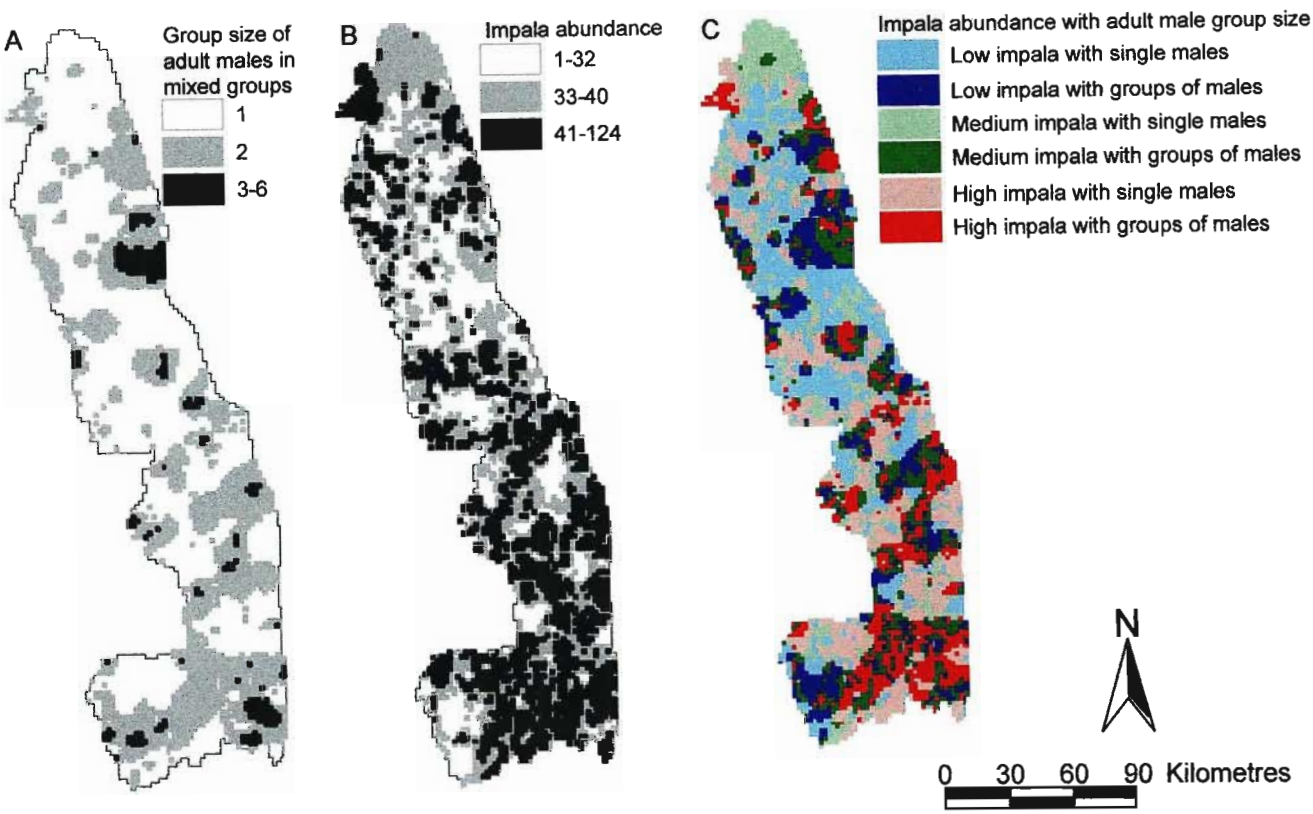

Figure 3.4. The surface map of group sizes of adult males in mixed groups (A) was contrasted with impala abundance (B). I used two categories of group size, either single or in a group, for ease of interpretation of the combination map (C). Adult males were in groups in most areas of high impala abundance and single in areas of low impala abundance (C). Grid cell size = one-minute^2.

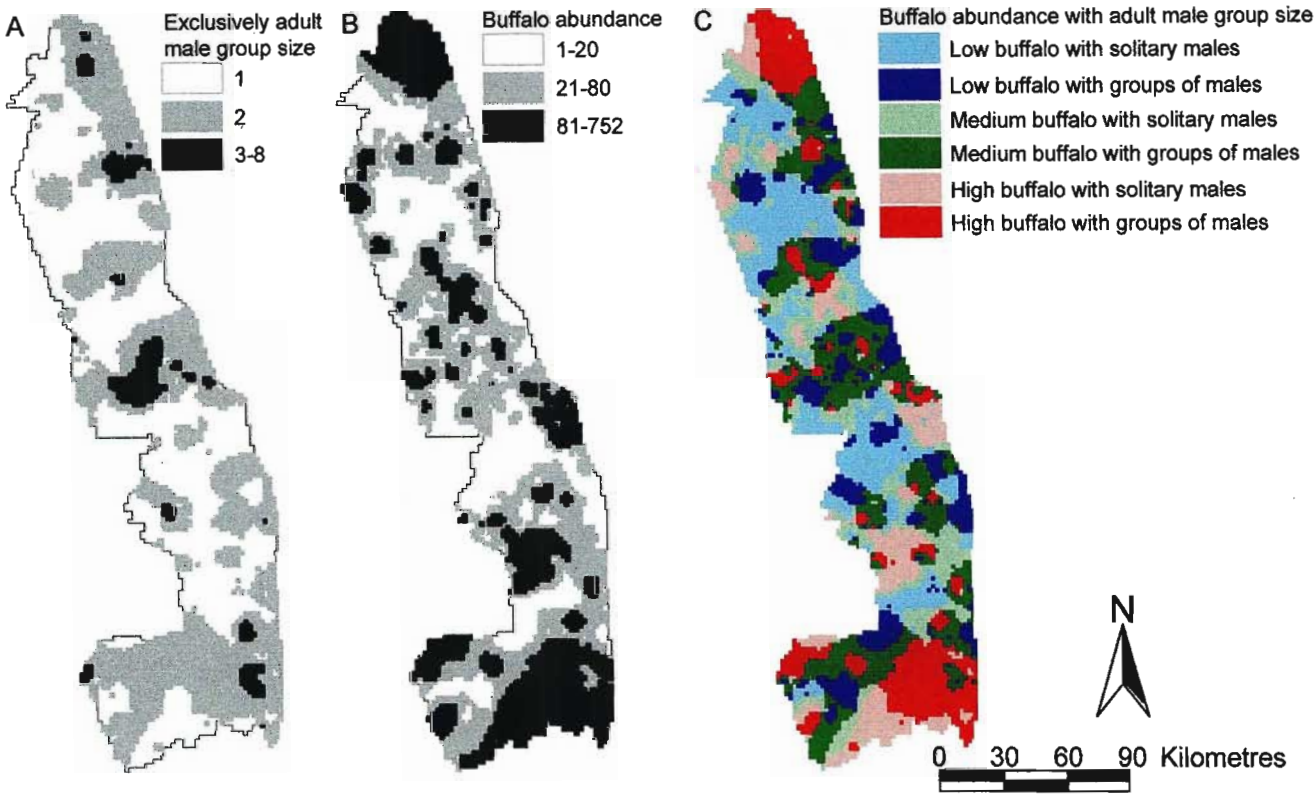

Figure 3.5. The surface map of exclusively adult male group sizes (A) was contrasted against the buffalo abundance surface map (B). I used two categories of group size, either solitary or in a group, for ease of interpretation of the combination map (C). Adult males were predominantly in groups in the areas of high buffalo abundance in the northern and southern sections of KNP (C). In the areas of low buffalo abundance adult males were predominantly solitary (C). Grid cell size = one-minute^2.

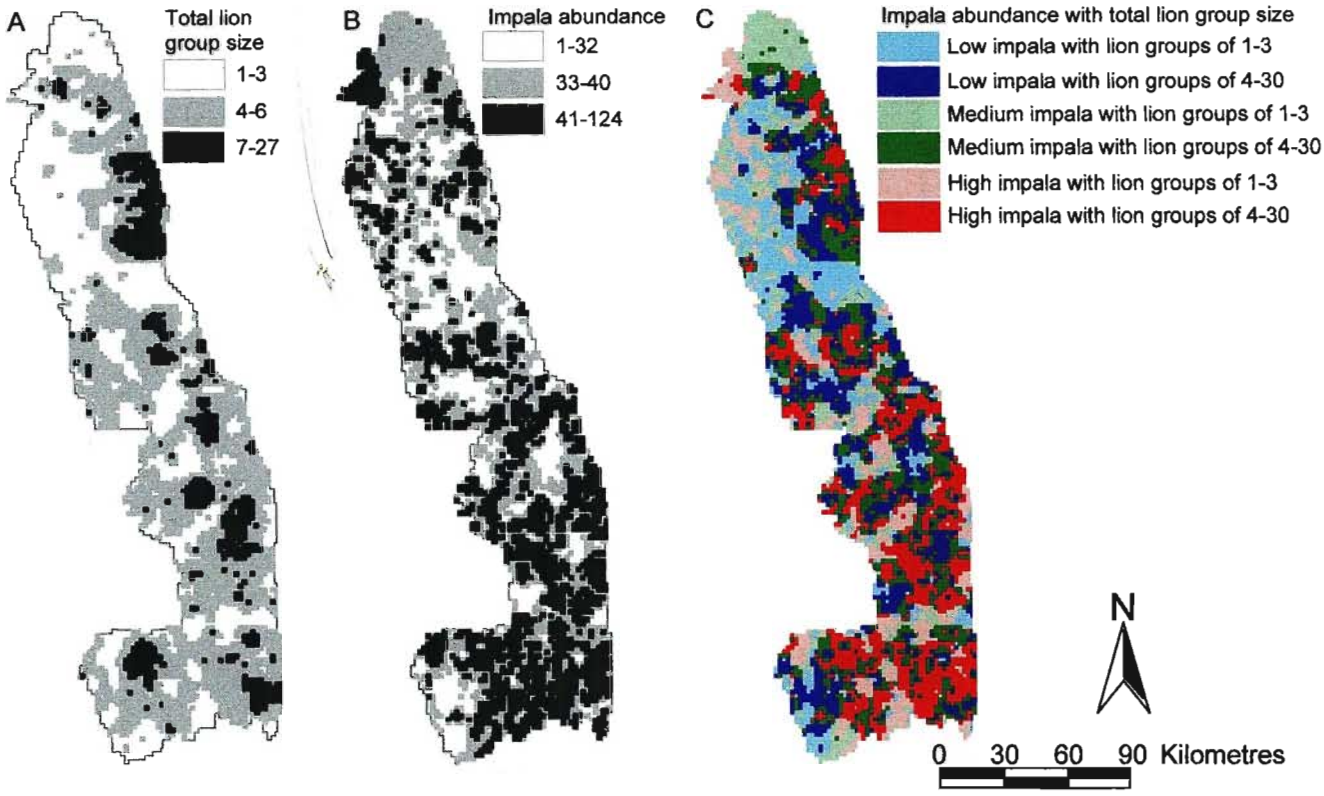

Figure 3.6. The surface map of total lion group size (A) was contrasted against the impala abundance surface map (B). I used two categories of group size for ease of interpretation of the combination map (C). Total group size therefore increased with increasing impala abundance (C). Smaller groups of lion were predominant in northern KNP, while larger groups predominated in the south (C). The surface maps have a grid cell size of one-minute^2.

Prey selection

Summary of all kill data

Table 3.7. I compiled a list of the species killed and eaten by lions in KNP as recorded in the ranger diaries and on the monthly predator returns from 1957 to 1985 only.

	Common Name	Scientific Name
1	Aardvark	*Orycteropus afer*
2	African buffalo	*Syncerus caffer*
3	African elephant (calf)	*Loxodonta africana*
4	Black-backed jackal	*Canis mesomelas*
5	Blue wildebeest	*Connochaetes taurinus*
6	Burchell's zebra	*Equus burchelli*
7	Bushbuck	*Tragelaphus scriptus*
8	Bushpig	*Potamochoerus porcus*
9	Cape pangolin	*Manis temmincki*
10	Cape porcupine	*Hystrix africaeaustralis*
11	Chacma baboon	*Papio cynocephalus*
12	Common duiker	*Sylvicapra grimmia*
13	Eland	*Taurotragus oryx*
14	Giraffe	*Giraffa camelopardalis*
15	Hippopotamus (young)	*Hippopotamus amphibius*
16	Impala	*Aepyceros melampus*
17	Kudu	*Tragelaphus strepsiceros*
18	Lichtenstein's hartebeest	*Sigmoceros lichtensteini*
19	Nyala	*Tragelaphus angasi*
20	Ostrich	*Struthio camelus*
21	Reedbuck	*Redunca arundinum*
22	Roan antelope	*Hippotragus equinus*
23	Sable antelope	*Hippotragus niger*
24	Spotted hyaena	*Crocuta crocuta*
25	Springhare	*Pedetes capensis*
26	Steenbok	*Raphicerus campestris*
27	Tortoise	*Geochelone pardalis*
28	Tsessebe	*Damaliscus lunatus*
29	Warthog	*Phacochoerus aethiopicus*
30	Waterbuck	*Kobus ellipsiprymnus*
31	Wild dog	*Lycaon pictus*

Note: Common names and scientific names after Mills & Hes (1997).

Although lions were generally not noted to have eaten hyaena that they killed, there were a few incidences recorded where the lions ate the hyaena, hence I have included it on the prey list (Table 3.7). Although lions were also observed to have killed a number of domestic animals, including a dog, hens, goats, cattle, donkeys and horses, these have not been included in the table.

I have illustrated the proportion of species killed by lions from 1957 to 1985 in terms of abundance (Fig. 3.7A) and biomass (Fig. 3.7B). I grouped the following species together as "other" prey species for both figures: aardvark, baboon, bushbuck, bushpig, duiker, eland,

elephant calves, hippopotamus, nyala, ostrich, porcupine, reedbuck, roan, sable, spotted hyaena, springhare, tortoise, tsessebe and warthog. I did not include tortoise in the biomass calculations. In terms of the proportion of each species in the diet, when buffalo proportion was high, the proportions of zebra and wildebeest were lower and vice versa (Fig. 3.7A). The presence of waterbuck in the diet varied between zero and 10%, while that of giraffe fluctuated between zero and 20% (Fig. 3.7A). However, as the data are not complete, the zero values cannot be taken to mean that none of these species were killed in that year. Based on biomass, buffalo contributed more to the diet of lions annually than any other species except giraffe (Fig. 3.7B). When buffalo biomass in the diet was high, giraffe biomass was low and vice versa (Fig. 3.7B). Impala contribute very little to the diet, based on biomass. However, these results may be an artefact of the data set as prey species such as buffalo and giraffe are large and therefore conspicuous to the observer while impala will often be missed, as they are small and often completely consumed.

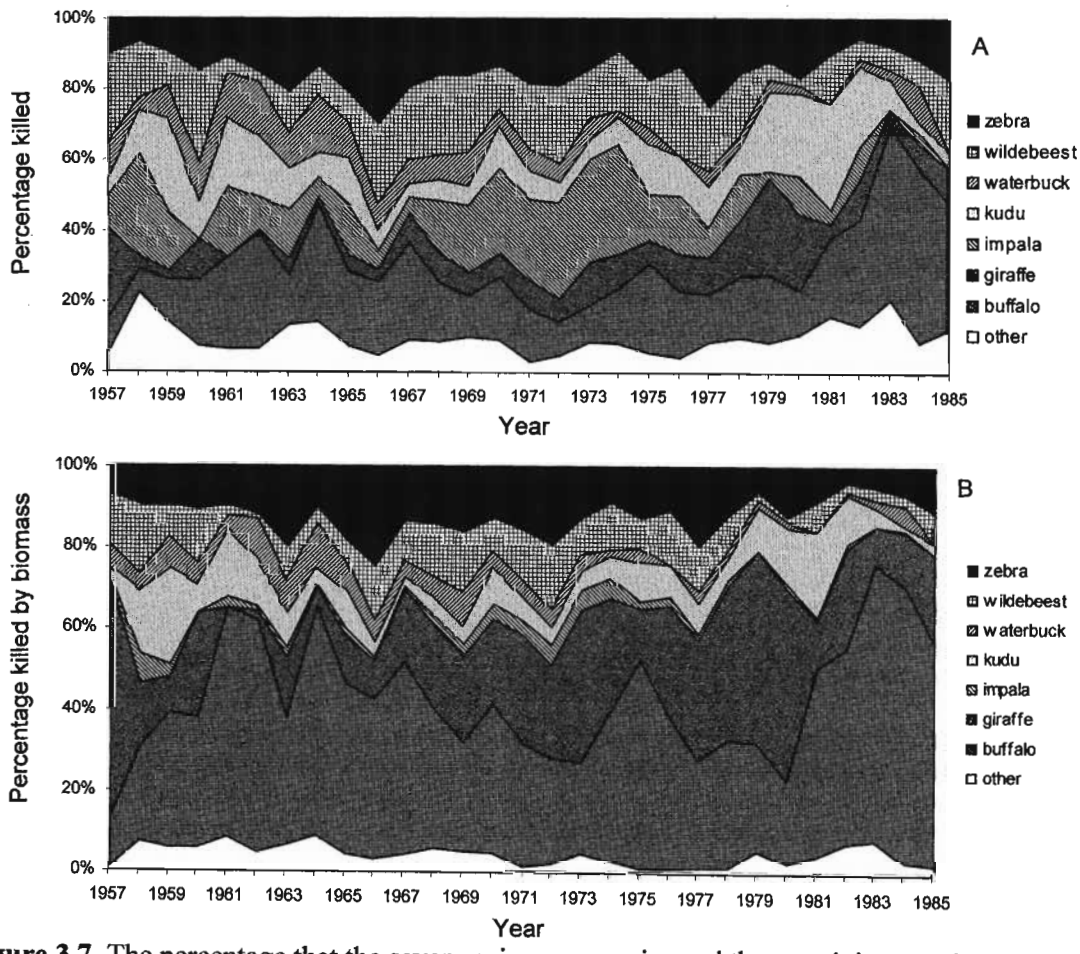

Figure 3.7. The percentage that the seven main prey species and the remaining species grouped together contributed to the diet of lions in KNP is illustrated in terms of actual kills (A) and the contribution by biomass (B) of each species. The prey species grouped together under "other" are listed in the main text.

Lion variables

Adult males

Adult male group size was significantly higher at buffalo, giraffe and wildebeest kills than at those of impala, kudu, waterbuck and zebra (Table 3.8; median group size of two versus one respectively, Fig. 3.8). Males are important in the successful capture of buffalo (Packer 1986; Funston *et al.* 1998). Therefore the males may be present as their full coalition size, as they have participated in the hunting of the larger prey.

The negative correlation between the proportion of giraffe available and the average group size of adult males in mixed group size was not significant (Table 3.9). The negative correlation between the proportion of kudu available and the average group size of adult males in mixed groups was also non-significant (Table 3.9). The distribution and group sizes of male coalitions may be influenced more by female lion distribution than by prey distribution. Females may not be as abundant in these areas as they may be more concentrated in the areas of their favoured prey such as wildebeest.

The average and maximum group sizes of exclusively adult male groups were correlated with the proportions of buffalo, giraffes, impalas, kudu and wildebeest available (Table 3.9). All correlations except that involving proportion of kudu available were significant (Table 3.9). These correlations were all negative, except for buffalo where the exclusively adult male group size increased with an increase in the proportion of buffalo available (Table 3.9; Figs 3.9.1 & 3.9.2). Males participate in the hunting of larger prey species such as buffalo, which could explain the presence of larger coalitions in areas of higher buffalo availability.

Adult females

The median adult female group size was significantly greater at the kills of buffalo and giraffe than at the kills of the other species (Table 3.8; Fig. 3.8). The largest group size was also recorded at a buffalo kill (eight; Fig. 3.8). Larger groups of females may be necessary to successfully hunt larger prey species while solitary hunters can successfully hunt smaller species such as impala. Larger carcasses also provide more food and therefore can support a larger feeding group size. A single female at the carcass of a large prey species may have been scavenging from another group's kill or could have been a subadult mistakenly identified as an adult lioness.

The average group sizes of adult females in mixed groups and exclusively adult female groups were not significantly correlated with any of the proportions of prey available (Table 3.9). The vulnerability of the available prey species may be more important than their abundance.

Subadults

Subadult group size was significantly lower at impala and kudu kills than at those of other species (Table 3.8; Fig. 3.8). Impala are small prey animals that only provide a small amount of food per animal. Therefore, I would expect smaller groups to be present at these kills than at larger kills.

Average subadult group size was positively correlated with the proportion of zebra available; however, this correlation was not significant (Table 3.9).

Cubs

Cub group size did not differ significantly between the kills of different species, with a median group size of three for five of the seven species (Table 3.8; Fig. 3.8).

Although a positive correlation coefficient was determined for the relationship between the average cub group size and the proportion of impala available, the correlation was not significant (Table 3.9).

Cub: adult female ratio

The cub to adult female ratio was correlated with the proportion that impala contributed to the total species composition, although this correlation was not significant (Table 3.9).

Total group size

The median total group size was significantly higher at giraffe kills than at kills of other prey species (Table 3.8; Fig. 3.8). The ranges of group sizes was also greatest for giraffe and buffalo kills which are the two largest prey species considered in this study (Fig. 3.8). Larger groups may be necessary to successfully hunt larger prey species while larger carcasses also allow for larger feeding group sizes. The lowest median group size was for impala (one, Fig. 3.8) which may result because not only do smaller prey animals provide less food, but solitary individuals can also successfully hunt them.

The average total group size was not correlated with the availability of any of the seven prey species.

Table 3.8. Lion group size should be largest at kills of larger prey species, as larger foraging groups are required to successfully hunt larger prey. In addition, group sizes may be bigger at larger carcasses, as these will supply more food per capita than a small prey animal. The Kruskal-Wallis results comparing group sizes at the seven prey species generally agree with this idea.

Lion variable	χ^2	P
Adult males [a]	86.23	< 0.001
Adult females [a]	67.89	< 0.001
Subadults [a]	14.68	0.02
Cubs [a]	8.10	ns
Total group size [b]	175.55	< 0.001

Df = 6 in all cases.

Note: The critical significance levels have been adjusted as the data were used in multiple tests (Schork & Remington 2000). The adjusted critical P values are: [a] P = 0.025; [b] P = 0.01

Results where P ≥ 0.1 are indicated as ns (non significant), although only results with P < critical level have been interpreted as significant.

Table 3.9. The proportion of favoured prey species in the total prey available may influence lion group dynamics. I therefore tested for correlations between the lion variables and the proportional contribution of each of the seven prey species to the total number of individuals available using Spearman correlation analysis. Only those prey species and lion variables for which at least one significant result was obtained have been included in the table. Results for which $P \geq 0.1$ have been excluded.

Lion variables	N[1]		Proportion Buffalo		Proportion Giraffe		Proportion Impala		Proportion Kudu		Proportion Wildebeest		Proportion Zebra	
			r_s^2	P	r_s^2	P	r_s^2	P	r_s^2	P	r_s^2	P	r_s^2	P
Adult males in mixed groups [a]	397	average			-0.107	0.032			-0.09	0.074				
Exclusively adult males [a]	276	average	0.168	0.005	-0.159	0.008	-0.186	0.002	-0.122	0.042	-0.145	0.016		
Exclusively adult females [b]	105	average	0.186	0.057			-0.216	0.027						
Subadults [c]	114	average											0.191	0.042
Cubs [d]	97	average					0.187	0.066						
Cub : adult female [e]	95	ratio											-0.227	0.027

[1] N = sample size

[2] r_s = Spearman's correlation coefficient

Note: the critical significance levels have been adjusted as the data were used in multiple tests (Schork & Remington 2000). The adjusted P values are: [a] P = 0.017; [b] P = 0.013; [c] P = 0.025; [d] P = 0.017; [e] P = 0.01

Results for which $P \geq 0.1$ have been excluded, although only results with P< critical level have been interpreted as significant.

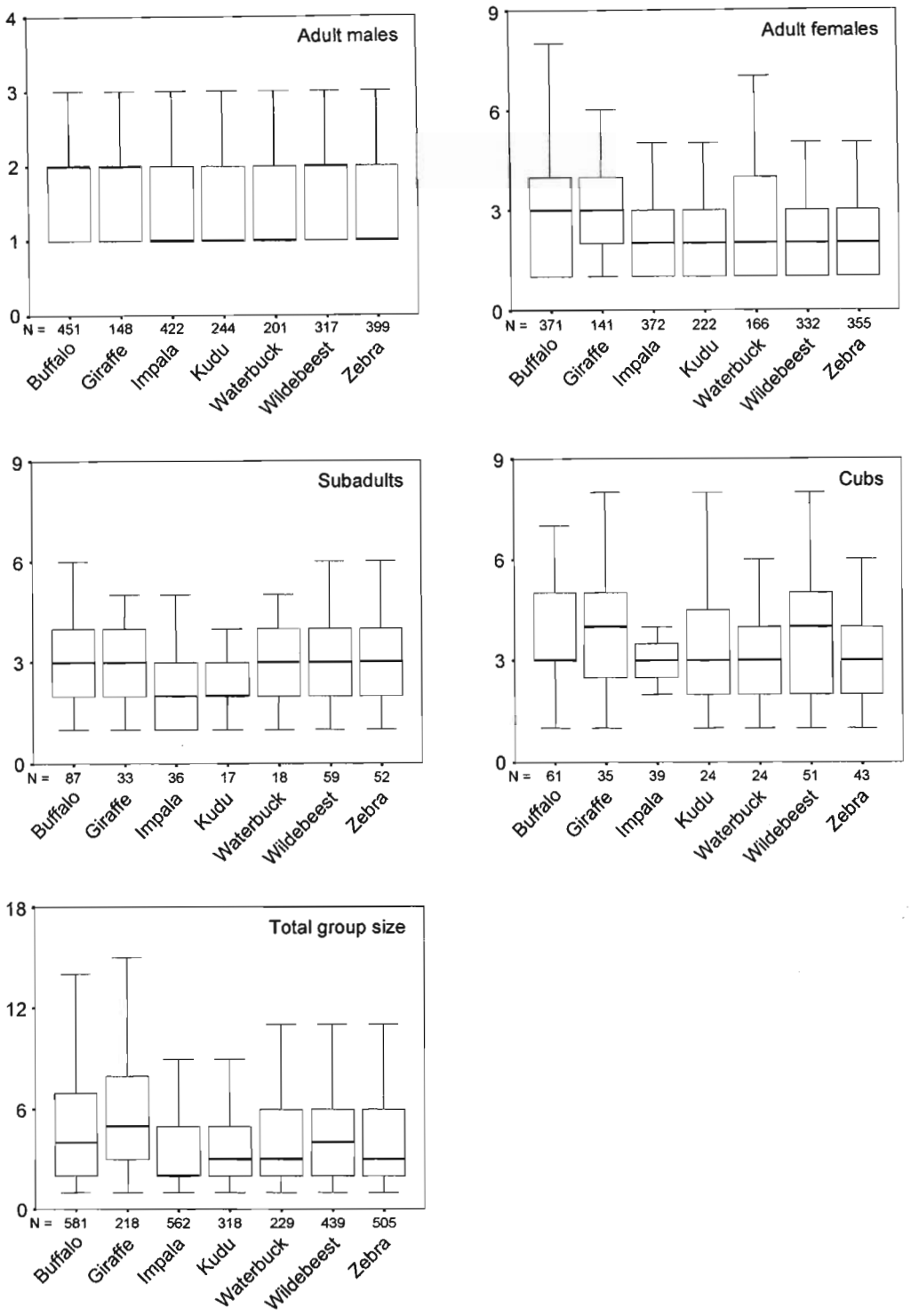

Figure 3.8. Group size of all lion variables was greatest at the kills of larger prey species. The box plots show the median, first and third quartiles and the range of the data. Only the maximum group size has been presented as the results for the average data follow a similar trend. N = number of cells with data.

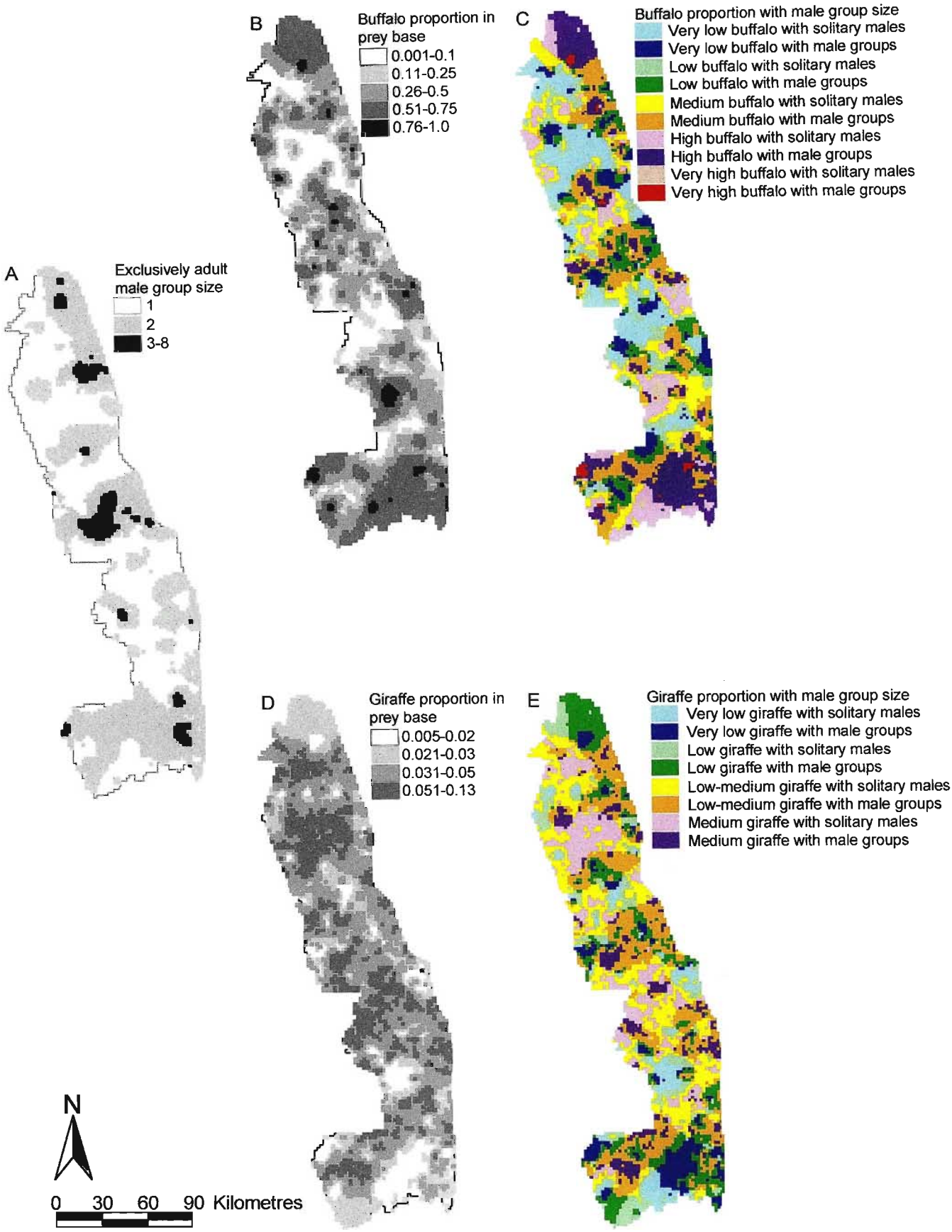

Figure 3.9.1. The surface map of exclusively adult male average group size (A) was contrasted with the proportions of buffalo (B) and giraffe (D) in the total prey base. I used two categories of group size, either solitary or in a group, for ease of interpretation of the combination maps (C & E). Adult males were solitary in areas of low buffalo proportion and in groups at high buffalo proportion availability (C), while this pattern was reversed for giraffe proportional availability (E).

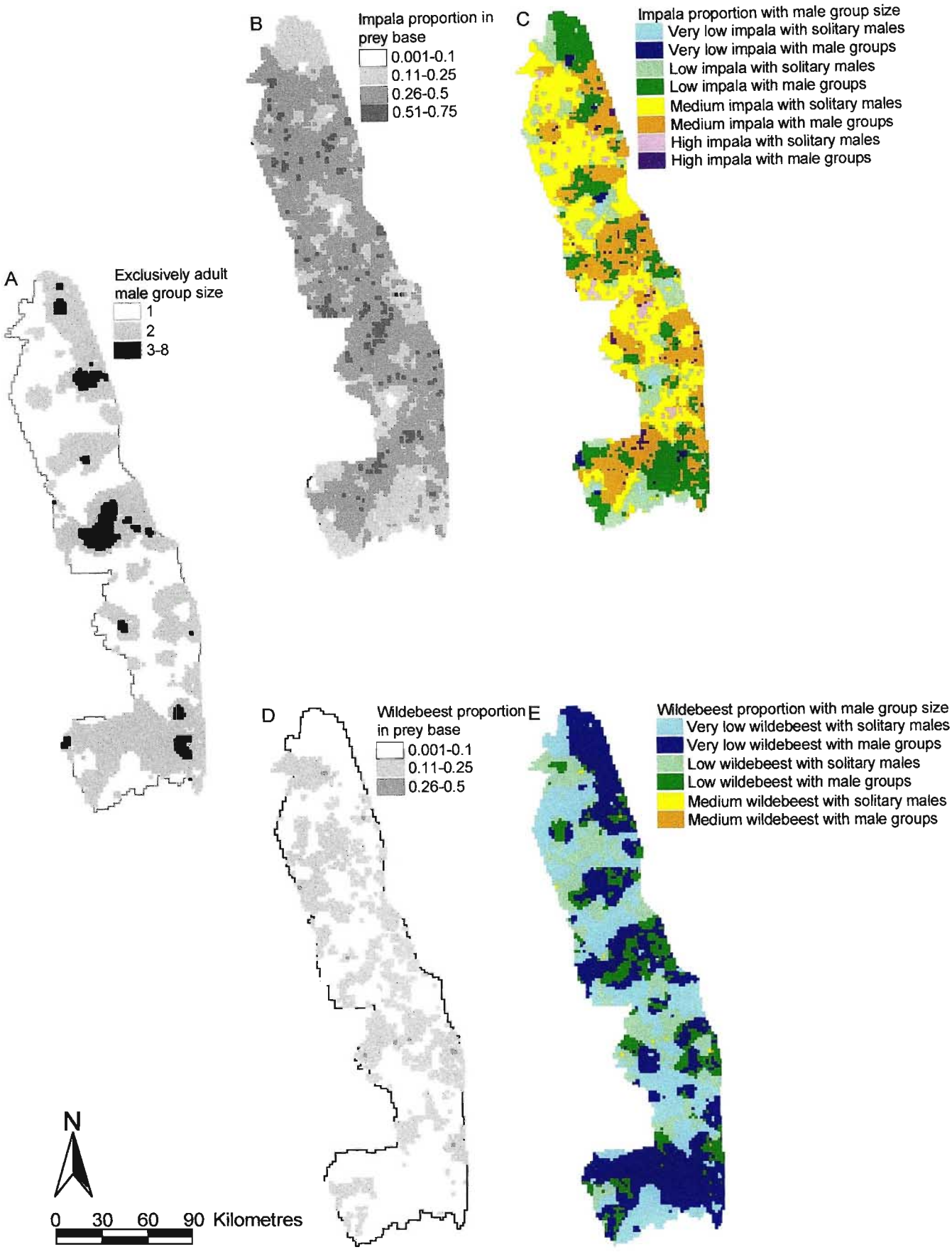

Figure 3.9.2. Exclusively adult male average group size (A) was negatively correlated with the proportion of impala (B) and wildebeest (D) in the total prey base. I used two categories of group size, either solitary or in a group, for ease of interpretation of the combination maps (C & E). Adult males were in groups at low impala (C) and wildebeest (E) proportional availability and solitary at high impala (C) and wildebeest (E).

Adult male: adult female ratio

The comparison between the number of observations of males only, females only and males and females together at the kills of buffalo and wildebeest was significant (G test. $G_{0.001,1} = 27.53$, P = 0.001; Fig. 3.10). Males, alone and together with females, were observed more often at buffalo kills than females, while the reverse was true for wildebeest kills, i.e. females both with and without males were observed more often at wildebeest kills. This result agrees with those of previous studies that have found buffalo to be important prey of males and wildebeest important to females (Rudnai 1974; Scheel 1993; Funston *et al.* 1998).

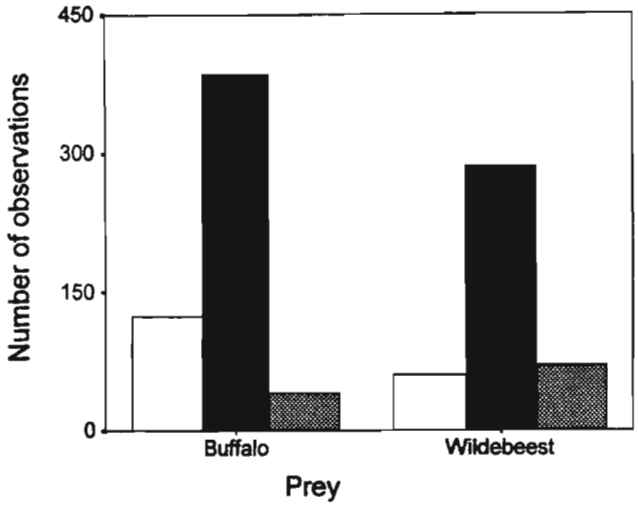

Figure 3.10. Males on their own and with females were seen at buffalo kills more often than females on their own, therefore implying that males are important in buffalo kills. The bar graphs show the number of observations of adult males on their own (open bar), adult females on their own (hatched bar) and when males and females were together (shaded bar) at the kills of buffalo and wildebeest.

Kill distribution versus prey abundance

There were no significant differences between the proportion of kills and the proportion abundance for any of the seven prey species, although the P values for giraffe and zebra were close to the significance level of $0.05 \geq P$ (Table 3.10). Unlike the data pertaining to the measurements of lion group sizes and composition, I did not apply the Bonferoni adjustment to the significance values, as the data have not been used in multiple tests. There were areas, however, where there were either proportionally more kills (red areas, Figs 3.11 – 3.17) or less kills (blue areas, Figs 3.11 – 3.17) than would have been expected according to the prey abundance (Figs 3.11 – 3.17).

Table 3.10. If lions kill prey according to their availability, one would expect there to be little or no difference between the number of kills and the abundance/ availability of that species. I found that proportionally the number of kills made by lions was similar to the abundance of each of the seven prey species studied. I compared the frequencies of kills and abundance over ten proportion categories using a Kolmogorov-Smirnov goodness-of-fit test.

Prey species	Z	P
Buffalo	0.894	ns
Giraffe	1.342	0.06
Impala	0.447	ns
Kudu	0.894	ns
Waterbuck	0.894	ns
Wildebeest	0.447	ns
Zebra	1.342	0.06

Results where $P \geq 0.1$ have been indicated as ns (non significant).

There were very few areas where the proportion of buffalo kills was exceptionally lower than the proportion of buffalo available (Fig. 3.11). In general, unlike the results obtained for the other prey species, there were proportionally more kills than expected over a large area (Fig. 3.11). Few giraffe kills were recorded, the majority occurring in the central and southern regions of KNP (Fig. 3.12). Impala kills were also generally lower than expected throughout KNP, however, impala are the most abundant herbivore in the park (Fig. 3.13). The areas where more kudu kills occurred generally fell along watercourses or near water sources (Fig. 3.14). There were very few, small areas where the proportion of waterbuck kills was exceptionally higher than the proportion of waterbuck available (Fig. 3.15). Although wildebeest are a common food source for lions, it was mainly in the central area of KNP, around Satara, that more kills were recorded than was expected according to their abundance (Fig. 3.16). More zebra kills were recorded in the central area of KNP which was similar for wildebeest (Figs 3.17 & 3.16, respectively). However, there were also areas spread throughout the park where more zebra kills took place than expected. However, most of these areas fall around the major camps in KNP, which may be an artefact of the data rather than a biological pattern (Fig. 3.17).

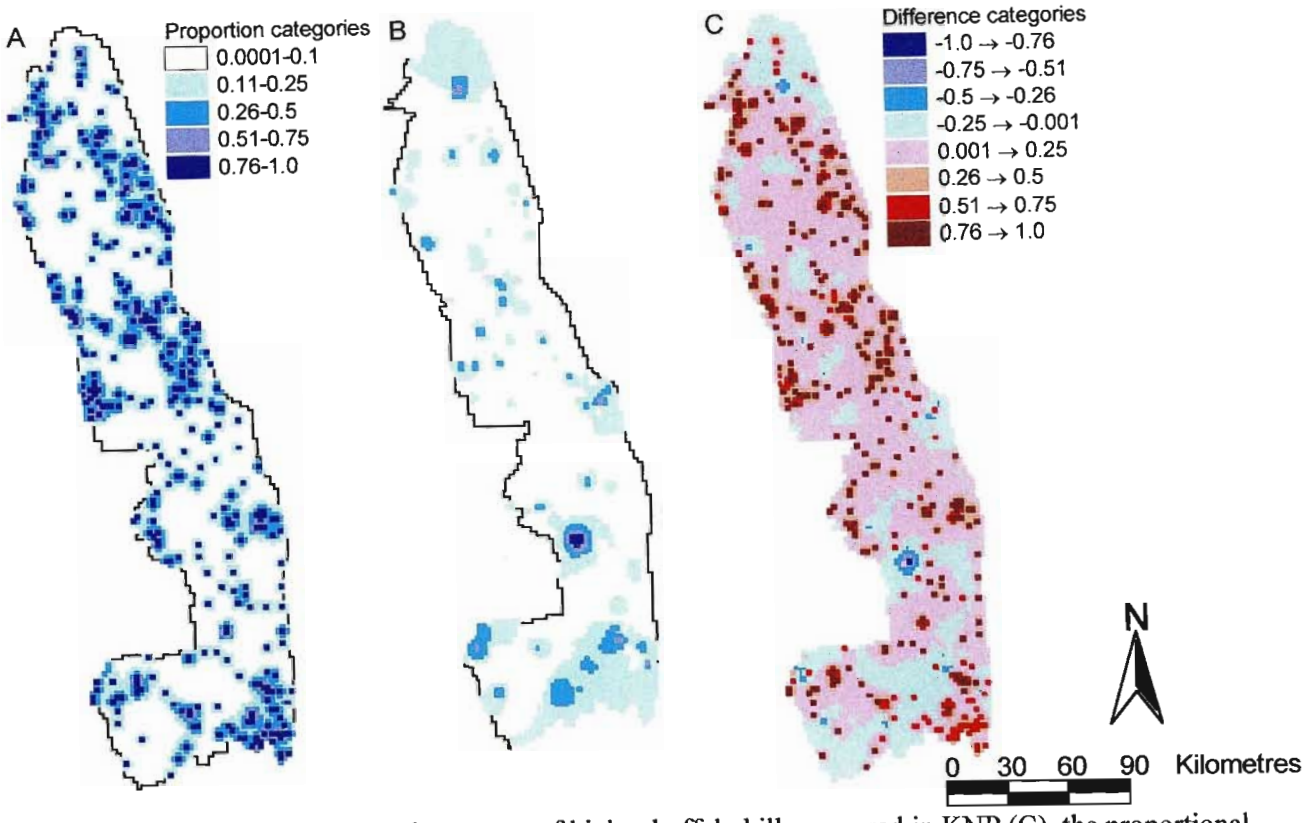

Figure 3.11. To determine where areas of higher buffalo kills occurred in KNP (C), the proportional abundance (B) was subtracted from the proportion of kills (A). There were more kills than expected in the areas of low buffalo availability suggesting that lions are selecting for buffalo in these areas (C).

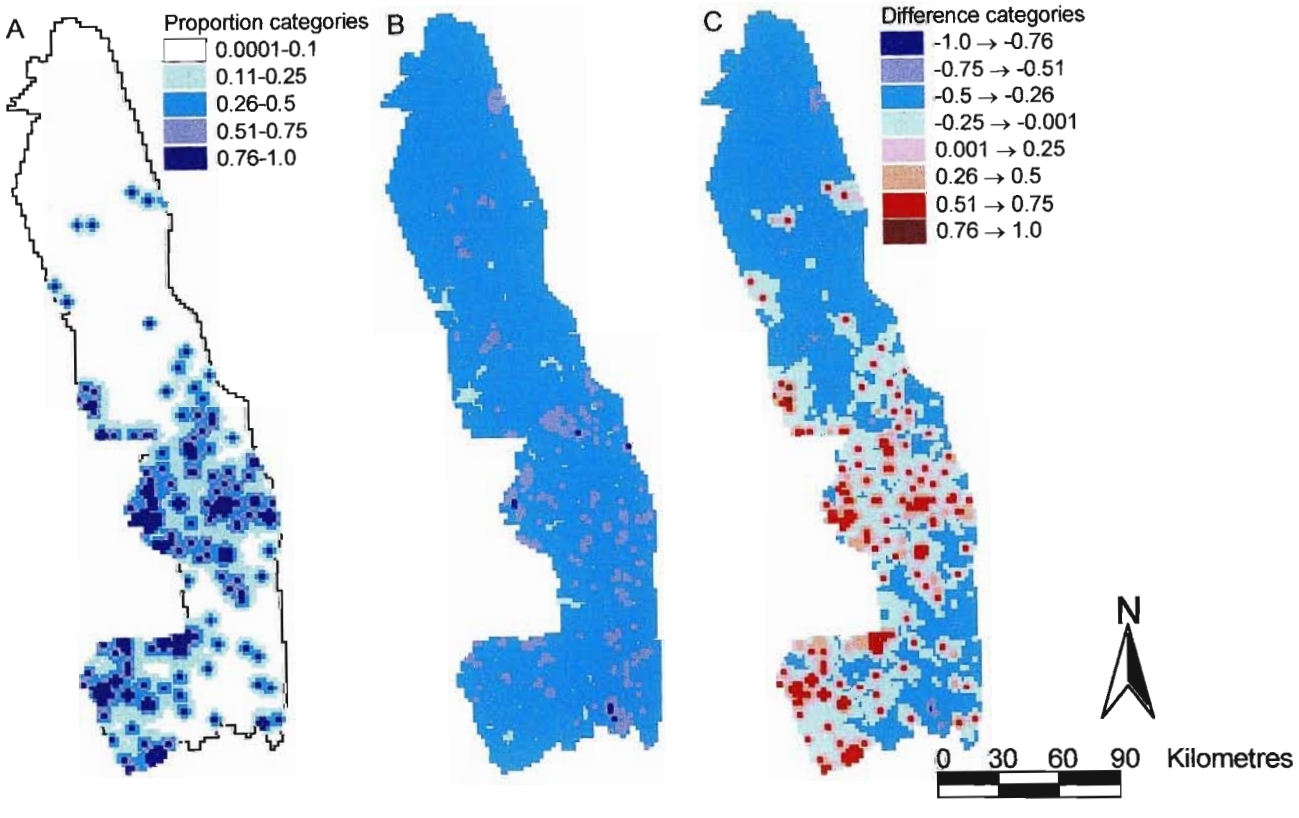

Figure 3.12. The giraffe proportion abundance map (B) was subtracted from the giraffe proportion kills map (A) to determine the distribution of kills compared to abundance (C). There were very few areas, mainly in the central and southern sections of KNP, where the proportion of kills exceeded the proportion abundance.

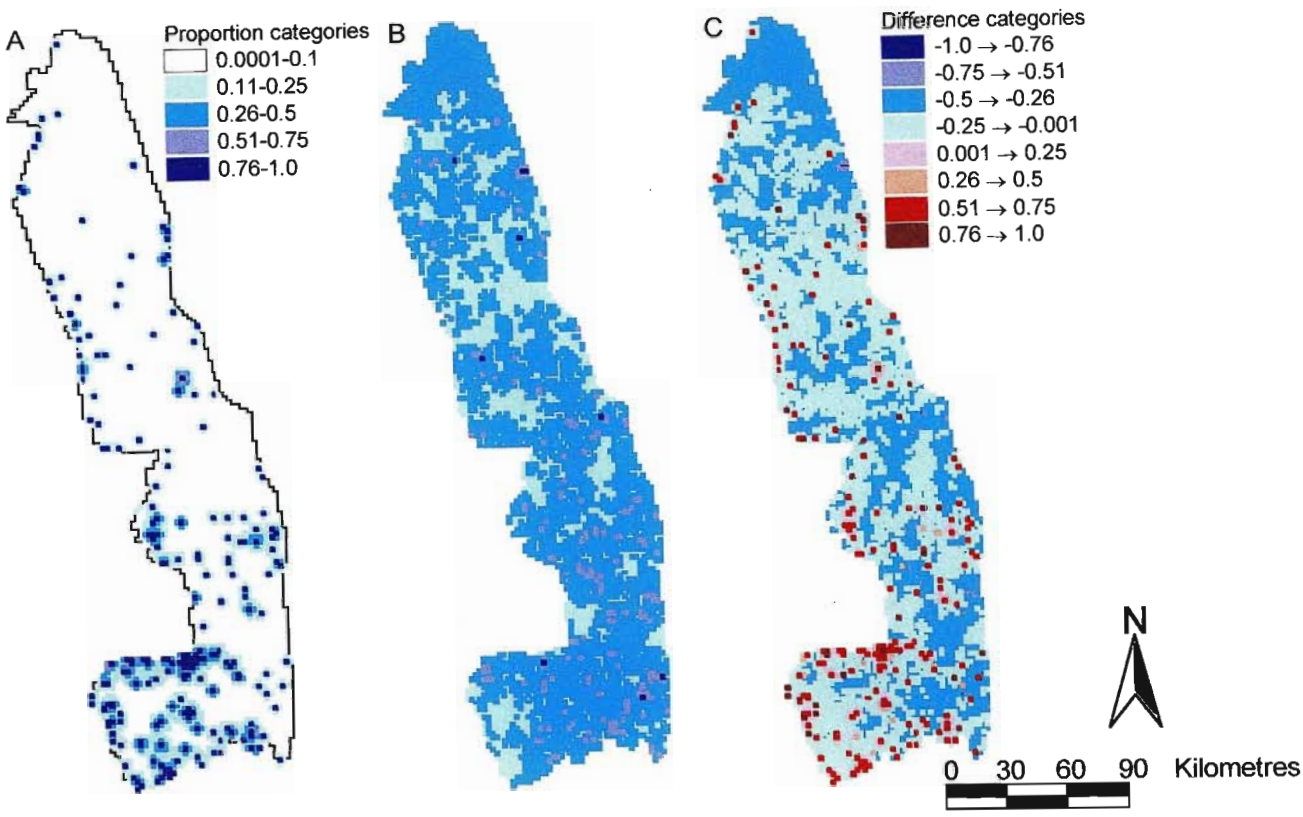

Figure 3.13. The impala proportion abundance map (B) was subtracted from the impala proportion kills map (A) to determine areas of higher than expected kills (C). There were very few areas where kills exceeded abundance, probably because impala are abundant throughout KNP.

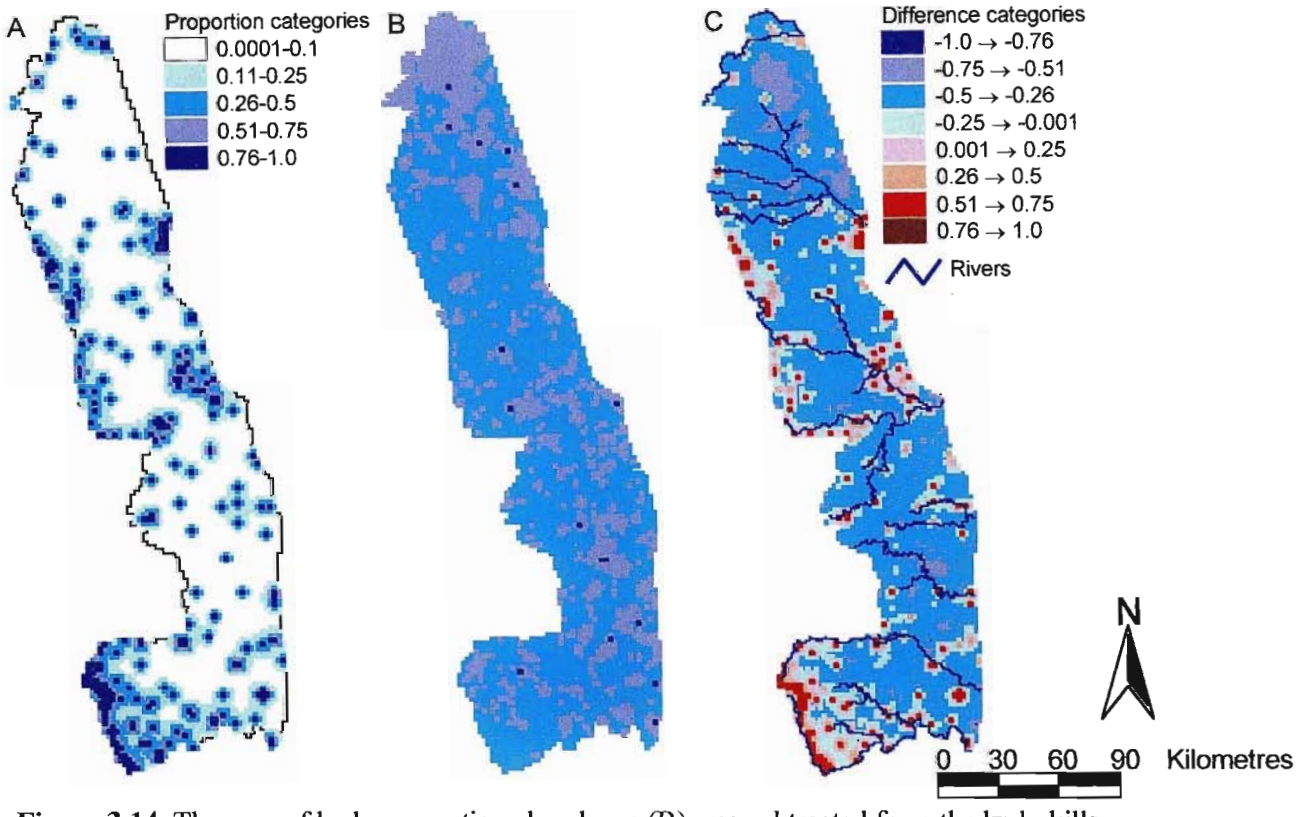

Figure 3.14. The map of kudu proportion abundance (B) was subtracted from the kudu kills proportion map (A) to determine the distribution of kills relative to kudu abundance (C). The areas where kills exceeded abundance were mainly along the river courses (C).

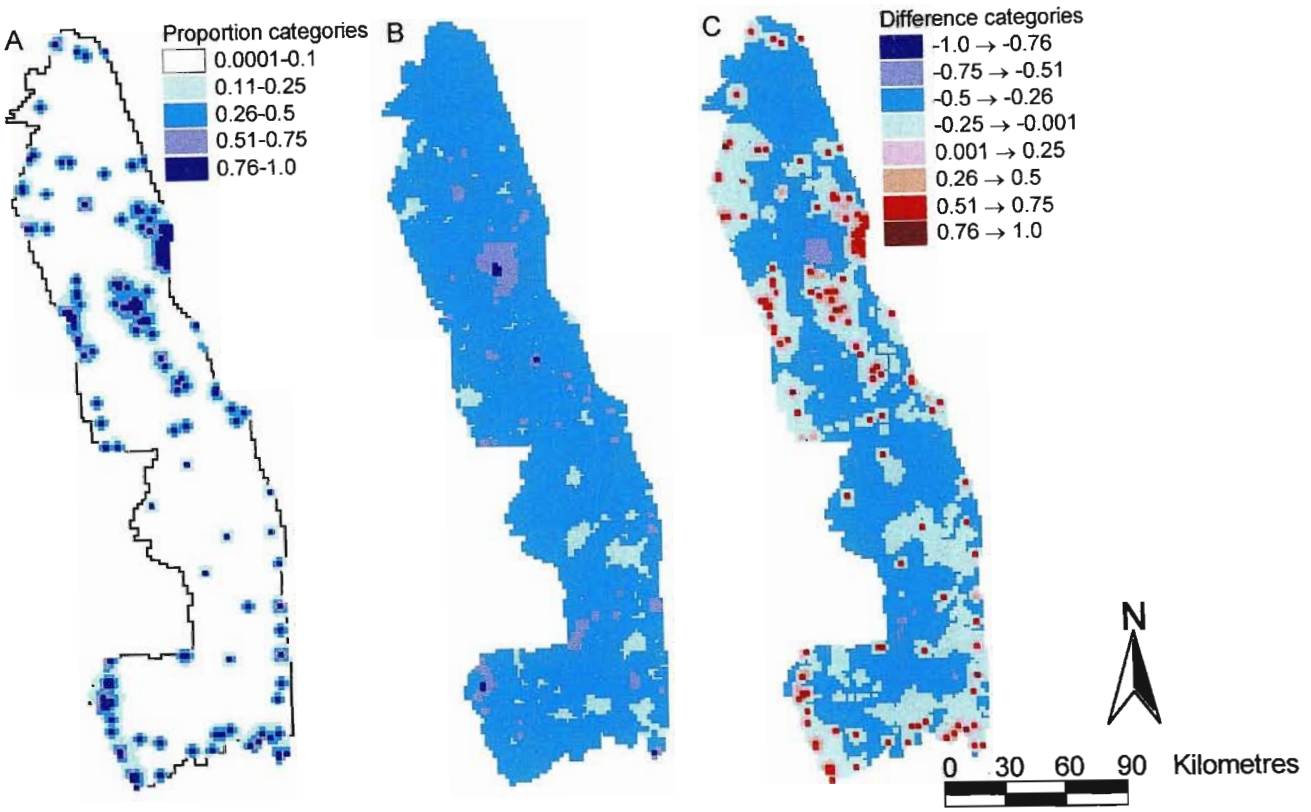

Figure 3.15. The map of waterbuck proportion abundance (B) was subtracted from the waterbuck kills proportion map (A) to determine areas of higher than expected kills (C). Throughout KNP, there were generally fewer kills than expected according to waterbuck abundance (C).

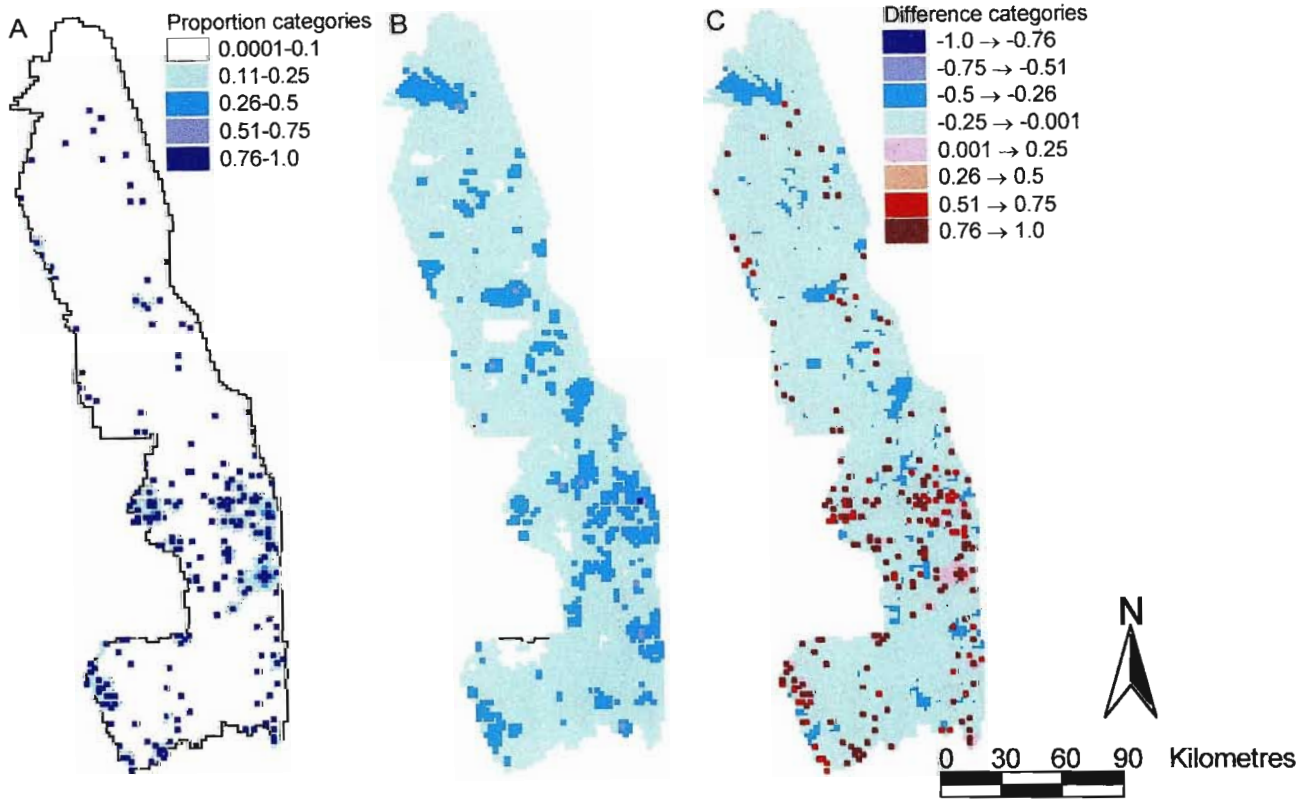

Figure 3.16. The wildebeest proportion abundance map (B) was subtracted from the wildebeest kills proportion map (A) to determine the distribution of kills relative to abundance (C). Areas where the proportion of kills exceeded the proportion abundance were concentrated in the central section of KNP (C).

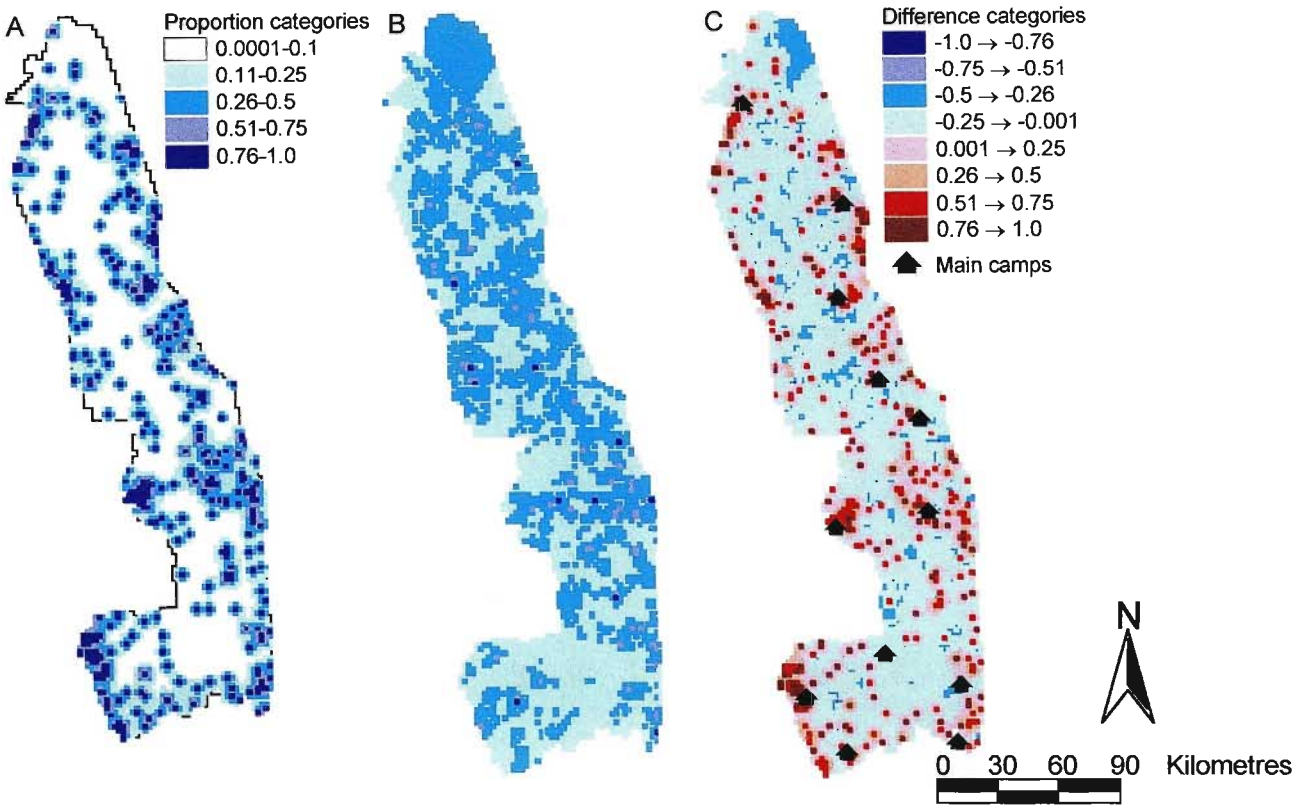

Figure 3.17. The map of zebra proportion abundance (B) was subtracted from the zebra kills proportion map (A) to determine areas of higher than expected kills (C). Most areas of greater than expected kills occurred in the areas around the main camps of KNP (C).

In summary, the results of prey selection have shown that larger groups were present at the kills of the larger prey species, with the exception of cub group size, which was not significantly different between the seven kill species. The presence of adult males and adult females differed between buffalo and wildebeest kills, which are their respective key prey species. Adult males were present at buffalo kills more often than wildebeest kills, while females were present most often at wildebeest kills. Buffalo proportion was important to adult males, but when adult males were in exclusively adult male groups only. Exclusively adult male group size increased with an increase in the proportion of buffalo in the prey base. Group size of exclusively adult males was negatively correlated with wildebeest proportion. Wildebeest are an important prey species of females, therefore territorial males may be associated with these areas. Exclusively adult male groups may therefore be avoiding these areas or remaining in smaller groups to remain relatively inconspicuous.

Discussion

Food is one of the most important resources influencing the survival, and thus the fitness of animals (Bergallo & Magnusson 1999). It is also an important driving force in group formation and thus sociality in carnivores (Macdonald 1983). Studies on social predators have shown that both distribution and group size are correlated with the density and availability of prey (Mills 1982; Macdonald 1983; Creel & Macdonald 1995; Meia & Weber 1996; Heinsohn 1997; Warrick & Cypher 1998; Andreka *et al.* 1999). Larger groups of predators occur where prey is more abundant (prey-rich areas) while groups are smaller where prey is limited or scarce (Creel & Macdonald 1995). However, Packer *et al.* (1990) found that smaller groups of lions formed when prey were abundant and larger groups when prey were scarce.

The RDH states that group sizes should be largest in areas of greater prey abundance and smaller in areas where prey are scarce (Macdonald 1983). However, my results based on biomass availability did not support this hypothesis, as lion group sizes did not differ significantly between areas of high and low biomass availability. This may mean that prey abundance is not driving group formation in lions, or that other factors relating to the prey available may be affecting group sizes. A number of studies have emphasised that it is not just the abundance of prey available that is important but more so the vulnerability of those species (Bertram 1973; Iriarte *et al.* 1990; Mills *et al.* 1995). Therefore while lions may be in an area of high prey biomass, the species contributing to that mass may not be ideal prey to the lions present. For example, although adult females in large groups can kill a buffalo, it is not their favoured prey species. Therefore when buffalo are in abundance and therefore contributing a large amount to the available prey biomass, it may be the presence of other species that is affecting female group sizes. However, in terms of females, Packer *et al.* (1990) determined that there were other factors apart from food determining group formation, such as cub and territory defence.

When I used individual prey species abundance to test the RDH, I found that some lion group types were influenced more significantly by certain prey species' abundance than others. Buffalo abundance was important to exclusively adult male groups, as I would have expected as a result of buffalo being one of their key prey species (Packer 1986; Funston *et al.* 1998). Adult male coalitions that were associating with mixed groups and adult females in mixed groups increased with an increase in the abundance of impala. Impala have been noted as an important food source to adult males in southern KNP (Funston *et al.* 1998) and to adult females (Rudnai 1974; Scheel 1993), which may explain the larger group sizes of males and females in areas of

higher impala availability. Wildebeest, have been noted as a preferred prey species of female lions (Rudnai 1974; Mills & Shenk 1992; Scheel 1993), yet my results did not show a correlation between these variables but rather that adult male group sizes increased with increasing wildebeest abundance. Male coalitions may be larger in these areas as they are associating with females. Larger coalitions have greater success defending their pride from competitive males than smaller coalitions (Bygott *et al.* 1979); therefore it may be advantageous for members of a coalition to remain together when they are in an area with high female density.

Neither subadult group size nor cub group size was influenced by the abundance of any of the seven prey species studied. The number of cubs surviving in the pride will affect subadult group size. Although nutrition and thus prey influence cub survival, previous work has found that regardless of size, litter productivity (cub survival) is not influenced greatly by prey availability (Packer & Pusey 1995). Subadults are capable of hunting from the age of two (Schaller 1972; Packer *et al.* 1990), but until they are evicted from the pride, their distribution will be influenced by that of their mothers.

In terms of prey selection by lions in KNP, although they kill a broad selection of species, certain species contribute more to the diet in terms of both numbers of kills and biomass. Buffalo, wildebeest and zebra were noted to be important species contributing substantially in number to the diet over the 29-year period, and fluctuating in relation to each other. When buffalo were the primary kill species, wildebeest and zebra kills were lower while this pattern was reversed when buffalo contribution to the diet was low. My results agreed with those of previous studies, which found buffalo to be more important to adult males and, wildebeest to adult females (Rudnai 1974; Mills & Shenk 1992; Scheel 1993; Funston *et al.* 1998). As in other studies, I also found group sizes to be largest at kills of larger prey species (Kruuk 1972; Van Orsdol 1984; Stander 1992a). However, my results refer to the feeding group sizes and not necessarily the hunting group sizes, which could differ vastly, especially when small cubs are present as they will only start participating in hunts from about two years of age (Schaller 1972; Packer *et al.* 1990).

Although my results (based on prey biomass) and those of studies on other predators have shown that prey is not the only factor affecting group formation, others have found data in support of the RDH, i.e. prey abundance drives predator group formation (Macdonald 1983; Packer *et al.* 1990; Creel & Macdonald 1995; Meia & Weber 1996). As I have discussed in Chapter Four, when prey is scarce, it may be more beneficial to form larger foraging groups

because it increases the possibility of attaining food. However, the counter argument would be that where food is in abundance, the area can support a larger group therefore it is viable to accept other individuals into the group. This may take the form of non-aggressive acceptance of conspecifics into the area (Meia & Weber 1996) or allowing juveniles to remain with the group. However, in this chapter I have found that neither explanation can explain the fact that group sizes do not substantially differ between areas of varying prey availability.

Prey size has been found to influence hunting group size for numerous predators (Kruuk 1972; Schaller 1972; Caraco & Wolf 1975). Therefore it appears to be an important factor driving group formation in predators. In areas where large prey are in abundance, it would therefore be beneficial for predators to form groups in order to increase hunting success and therefore fulfil the minimum daily requirements of the predators. Hunting in larger groups also facilitates the defence of food that might otherwise be scavenged by larger, more powerful predators (Carbone *et al.* 1997). However, where prey are small, it would be more beneficial to hunt alone, otherwise multiple hunts would be necessary to fulfil energy requirements.

In conclusion, while the RDH, prey size and selection may be used to explain group formation in certain areas or situations, there are also other factors that will influence group formation in lions. These include defence of cubs from infanticidal males and the defence of the pride territory (Packer *et al.* 1990).

CHAPTER FOUR
THE INFLUENCE OF RAINFALL ON LION GROUP DYNAMICS

Introduction

Rainfall is an important factor affecting population trends, either directly or indirectly (Taylor & Green 1976; Fichet-Calvet *et al.* 1999). A number of studies have shown relationships between herbivore populations and rainfall (e.g. East 1984; Sinclair, Dublin & Borner 1985; Mills *et al.* 1995). The total biomass of large savanna mammals is positively related to the mean annual rainfall in 20 wildlife areas of southern and eastern Africa, in which rainfall varied from less than 200 to more than 1100 mm.p.a. (East 1984). The density of wildebeest in the Serengeti was found to increase with the increase in rainfall in the dry season (Sinclair *et al.* 1985).

Rainfall also has indirect effects, for example, influencing predator ecology through changes in prey biology (Mills *et al.* 1995; Packer & Pusey 1995). The variance in leopard densities in sub-Saharan Africa have been explained by correlations with rainfall and hence with prey densities (Stander *et al.* 1997). Herbivore populations react differently to the rainfall cycles experienced in the Kruger National Park and as a result differ in their vulnerability to predation (Mills *et al.* 1995). Wildebeest and zebra are more vulnerable to predation by lions during the wet cycle, while buffalo and waterbuck are more vulnerable in the dry cycle (Mills *et al.* 1995).

Rainfall also affects habitat structure through its influence on vegetation structure (De Bie *et al.* 1998). Mitchell, Shenton & Uys (1965) recorded a total of 19 prey species taken by lions in the Kafue National Park, Zambia, of which buffalo were the most important. They observed that more buffalo were killed in the dry season than during the rainy season. They explained this by the structure of the habitat, saying that during the dry season there are more bush fires which reduce the cover normally supplied by grass, hence lions turn to buffalo which remain in the thickets and woodland. Note, however, that no significance measures were given to the trends.

Although studies have been done relating rainfall to herbivores and thus to predators, there has been little work done on whether rainfall variability influences lion group dynamics. Studies on other animals have shown that their foraging patterns and foraging groups change according to the variability of the food source - they either exhibit risk-prone or risk-averse behaviour (e.g. Caraco 1981a & b, 1982, 1983; Tuttle *et al.* 1990; Young *et al.* 1990). Although the rainfall in KNP undergoes rainfall cycles of below and above average rainfall, the amount of rainfall is not

the same throughout the park (Gertenbach 1980). As rainfall affects habitat structure, variable rainfall will result in a habitat with variable food resources.

In this chapter, my aim was to establish the effect of rainfall on lion group dynamics using the mechanism of risk-sensitive foraging to explain how rainfall variability acts to influence group dynamics. I hypothesised that group dynamics is influenced by variability in the environment. As previous studies have found it advantageous for lions to form larger groups when prey availability is variable or scarce (Packer *et al.* 1990; Stander 1992b), I predicted that larger groups would form in areas of more variable rainfall. I tested this prediction across (1) mean annual rainfall regions, (2) long-term variation in rainfall regions, and (3) seasons (wet and dry). Based on the mean annual rainfall, I carried out two tests, firstly, I compared lion group dynamics to the mean annual rainfall and secondly, I compared lion group dynamics between one year of extremely high rainfall and one year of extremely low rainfall.

Herbivores will be more widely distributed in areas of high rainfall, during high rainfall years and in the wet season as a result of the presence of surface water. This patchy prey distribution results in more variable prey availability because prey do not congregate around traditional lion ambush sites such as waterholes and rivers. There is thus a risk of lower searching success rate for the lions resulting in a lower successful hunting rate and hence a more variable energy-intake rate. Prey should be more vulnerable in the dry season and in areas of low rainfall as a result of poorer body condition; therefore all lion groups sizes should be equally successful in fulfilling their daily energy requirements condition. I therefore predicted that if risk sensitive foraging were the mechanism underlying lion group formation then (1) lion group sizes would be largest in areas of higher rainfall and smaller in areas of low rainfall. (2) Lions will form larger groups in the high rainfall year and smaller in the low rainfall year. (3) Lion group sizes will be largest in areas with a higher coefficient of variation in rainfall. (4) Lions will form larger groups in the wet season.

Methods

Rainfall data

Rainfall across KNP decreases from south to north with the exception of the area around Punda Maria in the north, which is at a higher altitude (Gertenbach 1980). There is a minor decrease in rainfall from west to east, following the decrease in altitude that is more pronounced towards the escarpment on the western boundary of the park (Gertenbach 1980; Fig. 4.1).

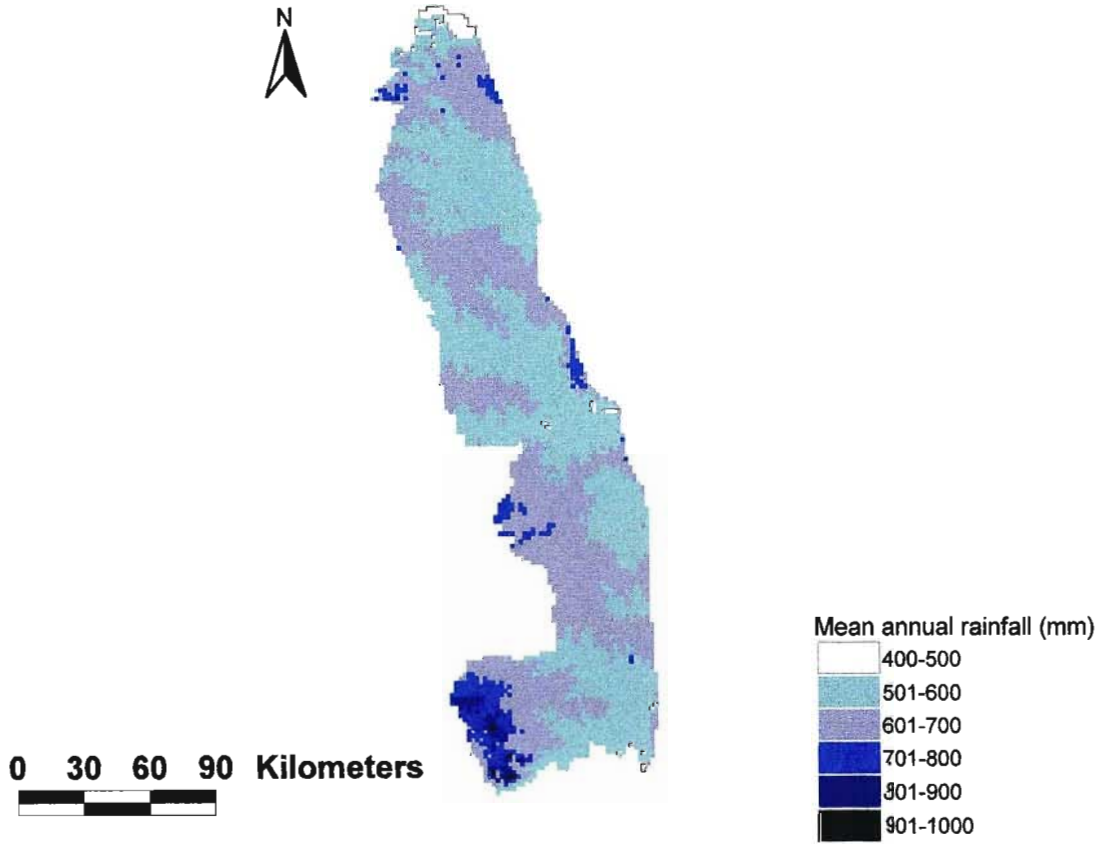

Figure 4.1. The mean annual rainfall map was created by averaging the 31 annual (July to June) rainfall maps from 1955/56 to 1985/86. Grid cell size = one minute².

The rangers in KNP record the rainfall data for their stations on a monthly basis. The Computing Centre for Water Research, Pietermaritzburg, South Africa, (CCWR) has captured these data, together with information from surrounding areas and farms. I obtained these data together with additional data for stations situated around KNP from the CCWR. I used these points of data to create annual rainfall maps on a one-minute² grid cell level. As rainfall is largely confined to the summer months (September to April)(Gertenbach 1980), I calculated the annual rainfall from 1 July to 30 June for each rainfall year from July 1957 to June 1985.

I only used data from the rainfall stations that had data for 85-90% of the period from 1957 to

1985 to create the rainfall maps. I carried out a regression analysis with rainfall as the dependent variable and longitude, latitude and altitude as the independent variables. The independent variables that were not significant ($P > 0.05$), i.e. not having an effect/ influence on the dependent variable, were removed and the regression redone. The resultant partial regression coefficients, together with maps of latitude, longitude and altitude, were used in the following equation to calculate the rainfall throughout the KNP on a minute^2 grid cell level for each year (28 maps created, Appendix 4.1):

Rainfall = c + (a * Longitude) + (b * Latitude) + (d * Altitude)

Where a, b and d are the regression coefficients for longitude, latitude and altitude respectively, and c is the regression constant determined separately for each year (P.V. Bolstad[1], pers. comm.).

Rainfall was not correlated with latitude in any of the years. It was always correlated with altitude and in 17 of the 28 years, it was correlated with both altitude and longitude.

Lion variables

I used the lion observation data from the monthly predator returns and the ranger diaries for the period from July 1957 to June 1985. I calculated the lion variables on a six monthly (April – September and October – March) and an annual basis (1 July - 30 June) to correspond with the two sets of analyses (seasonal and annual, respectively). Fifty-six seasonal (six-monthly) databases were created using the data from October 1957 until September 1985 and 28 one-year databases were created using the data from July 1957 until June 1985 (details of data, data capture and preparation are to be found in the general methods section of Chapter One). For each data set (seasonal and annual), the average, maximum and number of sightings of each variable for each grid cell was calculated resulting in one line of data for each cell reference for each period.

The following variables were determined:

1. adult males in:
    1.1. mixed groups
    1.2. exclusively adult male groups

[1] Dr P.V. Bolstad, University of Minnesota, Department of Forest Resources, 115 Green Hall, 1530 N. Cleveland Ave., St. Paul, MN 55108. Tel.: +1- 612-6251703 email: pbolstad@forestry.umn.edu

2. adult females in:
   2.1. mixed groups
   2.2. exclusively adult female groups
3. cubs
4. cub to adult female ratio
5. subadults
6. total group size

The maxima, averages and number of sightings were calculated for variables one, two, three, five and six above. Lions live in fission-fusion groups (Schaller 1972; Packer *et al.* 1990) where the pride splits into smaller subgroups that will group and separate over time. Average group size therefore reflects the size of the subgroups (from hereon referred to as groups) that lions form, while maximum group size may be a closer approximation of pride size. The cub to adult female ratio (variable four) was calculated using the maximum number of cubs recorded in the cell for each six month/ year period divided by the maximum number of adult females seen in that cell within that six month/ year period. The maximum adult female group size was taken as the absolute maximum of females recorded in that cell whether these females were in mixed groups or in exclusively adult female groups.

The average and maximum data for each variable were averaged over each of the three periods (annual, wet season and dry season) resulting in a final averaged average and averaged maximum map for each lion variable (15 annual maps and 30 seasonal maps). Hereafter I refer to the averaged average variables as average and the averaged maximum variables as maximum. The number of sightings for each variable was totalled for each cell for each period. The annual data were used to calculate the total number of sightings recorded in each rainfall variation category for each variable. The seasonal data were used to calculate the total number of sightings for each variable in each season.

I applied the Bonferroni adjustment to the significance levels used for each variable because the same data were used for multiple tests (Schork & Remington 2000). For each variable I calculated the P value as 0.05 divided by the number of tests that that variable and related variables had been used for (Table 4.1).

Table 4.1. I adjusted the significance levels for the lion variables used in all subsequent analyses based on the number of tests that each variable was used in or not independent of for each separate analyses. Thus for each group and sightings variable I included those tests for which the total group sizes or total group sightings were used, respectively.

Variable	Tests	Number of tests	P [a]
Adult male group sizes	Average and maximum adult males in mixed groups, average and maximum exclusively adult male group sizes, average and maximum total group sizes	6	0.008
Number of male sightings (across variability regions)	Habitat and road area categorical analyses for adult males in mixed groups, exclusively adult males and total groups	6	0.008
Number of male sightings (across seasons)	Categorical analyses for adult males in mixed groups, exclusively adult males and total groups	3	0.017
Adult female group sizes	Average and maximum adult females in mixed groups, average and maximum exclusively adult female group sizes, adult sex ratio, cub: adult female ratio, average and maximum total group sizes	7	0.007
Number of female sightings (across variability regions)	Habitat and road area categorical analyses for adult females in mixed groups, exclusively adult females and total groups	6	0.008
Number of female sightings (across seasons)	Categorical analyses for adult females in mixed groups, exclusively adult females and total groups	3	0.017
Subadult group sizes	Average and maximum subadult group sizes, average and maximum total group sizes	4	0.013
Number of subadult sightings (across variability regions	Habitat and road area categorical analyses for subadults and total group	4	0.013
Number of subadult sightings (across seasons)	Categorical analyses for subadults and total group	2	0.025
Cub group sizes	Average and maximum cub group sizes, cub: adult female ratio, average and maximum total group sizes	5	0.01
Number of cub sightings (across variability regions)	Habitat and road area categorical analyses for cubs and total group	4	0.013
Number of cub sightings (across seasons)	Categorical analyses for cubs and total group	2	0.025
Cub: adult female ratio	Average and maximum adult females in mixed groups, average and maximum exclusively adult females, average and maximum cub group sizes, cub: adult female ratio, average and maximum total group	9	0.006
Total group sizes	All the above mentioned variables related to group sizes	15	0.003
Total number of group sightings (across variability regions)	All the above mentioned variables related to number of sightings across variability regions	14	0.004
Total number of group sightings (across seasons)	All the above mentioned variables related to number of sightings across seasons	7	0.007

[a] P = Bonferroni adjusted critical P level for significance testing (Schork & Remington 2000).

Rainfall variability

In order to test whether risk-sensitive foraging could be used to explain how rainfall acts to influence lion group dynamics, I compared lion group size and composition with mean annual rainfall. I used the 15 final average, maximum and ratio lion variable maps for the analysis together with the averaged annual rainfall map (Fig. 4.1). As the data were not normally distributed (Kolmogorov-Smirnov test, $P < 0.05$ in all cases), a Spearman correlation was used to compare the averaged variables with rainfall (Zar 1999). Significance levels were adjusted using the Bonferroni adjustment (Schork & Remington 2000)(Table 4.1). Scatter plots were used to illustrate the significant correlations. I have only illustrated the results pertaining to the maximum lion variables, as these results were similar to those for the averaged variables.

I used the grid cell data from each annual rainfall map to determine in which year the rainfall was greatest and in which it was lowest. I used the two maps that had the majority of cells that were either highest or lowest in rainfall value for the extreme wet and extreme dry years, respectively. These were 1971/72 (high) and 1982/83 (low)(Fig. 4.2). I compared the averaged and maximum lion variables for each of these years. As the data were not normally distributed (Kolmogorov-Smirnov test, $P < 0.05$ in all cases), a Kruskal-Wallis one-way ANOVA was used to compare the lion variables among years (Zar 1999). The test variables were the fourteen averaged and maximum lion variables for each year and the grouping variable was rainfall year (minimum = 1 [low rainfall year: 1982/83]; maximum = 2 [high rainfall year: 1971/72]). Significance levels were adjusted using the Bonferroni adjustment (Schork & Remington 2000)(Table 4.1). I used box-and-whisker plots to illustrate the data showing the median, first and third quartiles and the range. Although, outliers and extremes were used in the analyses I have not represented them in the box plots, in order to avoid cluttering and to facilitate interpretation of trends. I have only illustrated the results pertaining to the maximum lion variables, as these results were similar to those for the averaged variables.

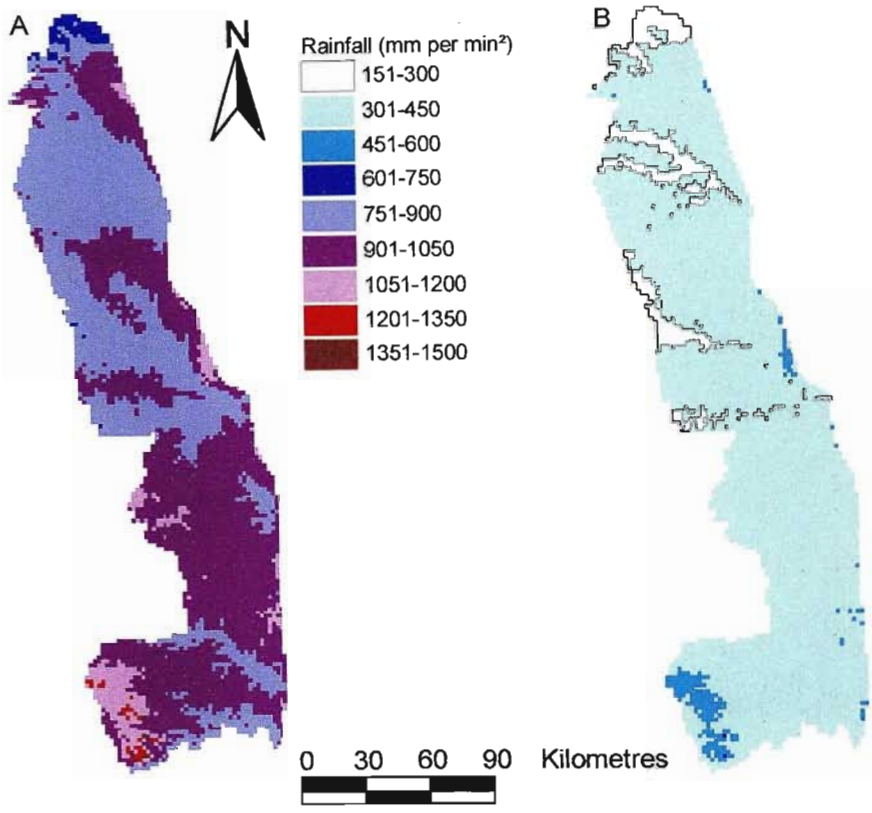

Figure 4.2. Between the period 1957 – 1985, the annual rainfall was greatest in 1971/72 (a) and lowest in 1982/83 (b). Map grid size = one min².

To determine if long-term variability in rainfall influenced lion group dynamics, I calculated the coefficient of variation in the rainfall experienced in each cell for the 28-year period in order to create a map of the variation in rainfall experienced in KNP. The coefficient of variation in rainfall over the 28-year period ranged from 24 to 33%, the most variability occurring along the south-eastern and extreme northern borders and the lowest variability occurring in a region in the south-western section of the park between Pretoriuskop and Malelane (Fig. 4.3).

Preliminary analysis indicated that the coefficient of variation divisions could be combined into three biologically meaningful categories, namely, low variation (24-25%), medium variation (26-29%) and high variation (30-33%). The data from each of the final 15 averaged lion variable maps were extracted into spreadsheets for further analyses. As the data were not normally distributed (Kolmogorov-Smirnov test, $P < 0.05$ in all cases), a Spearman correlation was used to compare the averaged variables in each rainfall variation category (Zar 1999). Significance levels were adjusted using the Bonferroni adjustment (Schork & Remington 2000)(Table 4.1). Scatter plots are used to illustrate the significant correlations. I have only illustrated the results pertaining to the maximum lion variables, as these results were similar to those for the averaged variables.

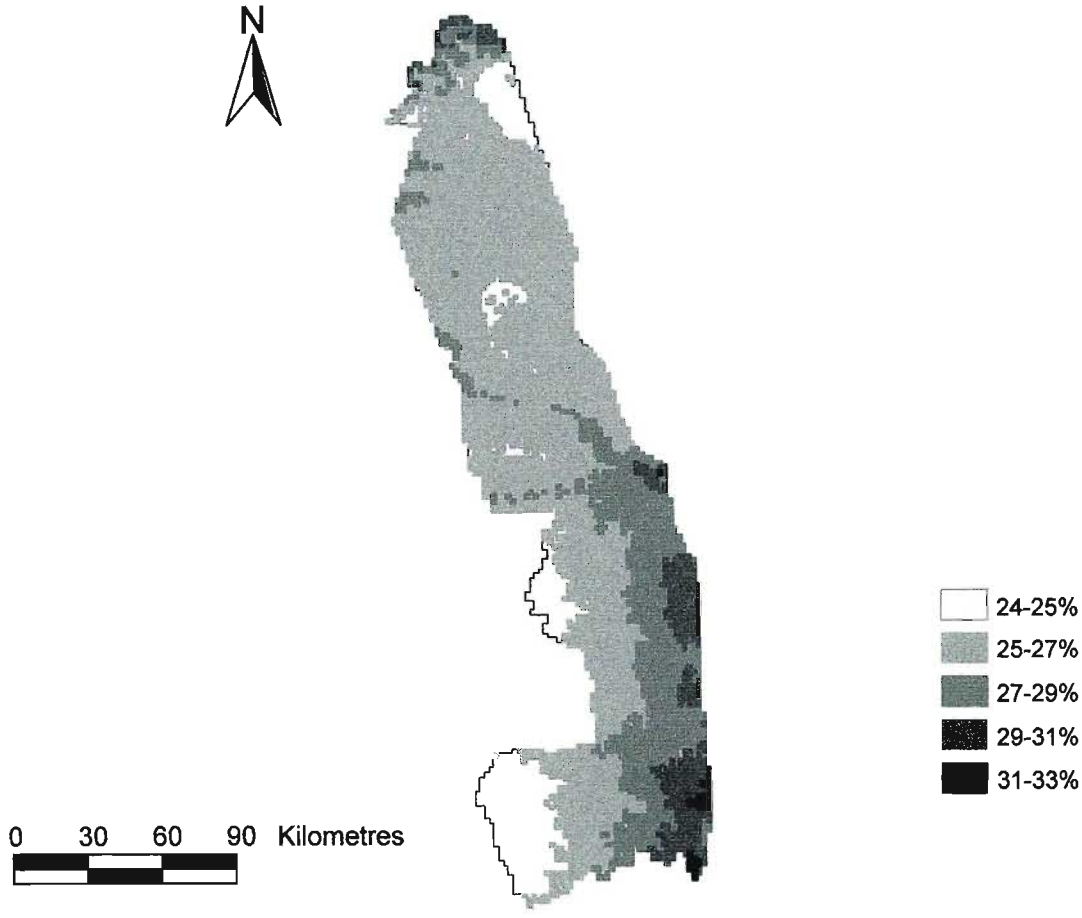

Figure 4.3. The coefficient of variation in rainfall across KNP, over the 28-year period from 1957-1985, ranged from 24 to 33%. Map grid size = one min².

Categorical analyses to test the difference between the total number of sightings for each variable recorded in each rainfall variation category were done using G-tests (Zar 1999) and are represented by bar graphs. As discussed in Chapter Two, the probability of an area being sampled was dependent on the road coverage, therefore I tested for differences between the categories based on the total area of each category as well as on the road coverage. Significance levels were adjusted using the Bonferroni adjustment (Schork & Remington 2000)(Table 4.1).

The effect of season on lion group dynamics

The data from each of the final 30 averaged variable maps were extracted into spreadsheets for further analyses. As the data were not normally distributed (Kolmogorov-Smirnov test, $P < 0.05$ in all cases), a Kruskal-Wallis one-way ANOVA was used to compare the averaged variables in each season (Zar 1999). The test variables were one of 15 dependent variables and the grouping variable was season (minimum = 1 [dry], maximum = 2 [wet]). Significance levels were adjusted using the Bonferroni adjustment (Schork & Remington 2000)(Table 4.1). I used box-

and-whisker plots to illustrate the data showing the absolute maximum, absolute minimum, mean and the first and third quartiles.

Season as a measure of visibility

One of my objectives, unrelated to the biological relationship between lion group dynamics and rainfall, was to determine if the number of sightings recorded in each season could be used as a measure of the visibility in that season. I predicted that there would be more sightings in the dry season not only because lions may be centred more around the waterholes, but also because the vegetation should be less dense, therefore visibility should be greater.

Categorical analyses to test the difference between the total number of variable sightings in each season were done using G-tests (Zar 1999) and are represented by bar graphs. As the data were divided into two seasons, I calculated the expected number of sightings to be 50% of the total number of sightings for each variable. Significance levels were adjusted using the Bonferroni adjustment (Schork & Remington 2000)(Table 4.1).

Results

Rainfall variability

Adult males in mixed groups

The correlations between the mean annual rainfall and the average and maximum group size of males in mixed groups were not significant (Table 4.2; Fig. 4.4). The average and maximum group sizes of adult males in mixed groups differed significantly between the years of high (1971/72) and low rainfall (1982/83)(Table 4.3). In both years, group sizes ranged between one and three with a median of one in the year of low rainfall and a median of two in the highest rainfall year (Fig. 4.5). This indicates that adult male coalitions were associating in mixed groups in the high rainfall year whilst being more likely to be on their own in the low rainfall year. Although adult male group size does not appear to be influenced by long-term rainfall, it may be influenced more on a short-term basis.

There were positive correlations between the variation in rainfall and the average and maximum group size of males in mixed groups, but only the average group size result was significant (Table 4.4; Fig. 4.6). Although the average number of adult males in mixed groups increased with the increase in rainfall variation, this was a relatively small increase as indicated by the low Spearman's correlation coefficients (Table 4.4). This result indicates a risk-prone reaction to greater variability in the environment, i.e. larger groups forming where conditions are more variable. The categorical analyses were significant when based on both the areas of the variation regions as well as the road coverage in each area (Table 4.5). There were more recorded sightings of adult males in mixed groups than expected in the regions of lowest rainfall variability (low: 24-25%, Fig. 4.7) as well as in the areas of higher variability (high: 30-33%, Fig. 4.7). Although these regions cover the smallest areas, they do occur along the boundaries of the reserve (Fig. 4.3) which would be patrolled by staff more often than more central areas (Gus Mills[2], pers. comm.).

Exclusively adult male groups

Neither the average nor maximum exclusively adult male group sizes was correlated with average annual rainfall (Table 4.2; Fig. 4.4). The average and maximum group size of exclusively adult males also did not differ significantly between the years of high (1971/72) and low rainfall (1982/83)(Table 4.3; Fig. 4.5). Exclusively adult male group size therefore does not appear to be influenced by differences in either long-term or short-term rainfall.

[2] Dr M.G.L. Mills, Scientific Services, Private bag X 402, Skukuza, 1350, tel.: (013) 7354240.

The results of the Spearman correlation analysis were not significant for groups of exclusively adult male lions (Table 4.4), indicating that when adult male lions were in exclusively adult male groups, their group size was not influenced by changes in rainfall variability (Fig. 4.6). The results of categorical analyses were significant based on both the areas of the variation regions and on the road coverage in each area (Table 4.5). There were more recorded sightings of adult males in mixed groups than expected in the regions of lowest rainfall variability (low: 24-25%, Fig. 4.7) as well as in the areas of higher variability (high: 30-33%, Fig. 4.7). Again, this may be as a result of the KNP borders being patrolled by staff more often than the central areas.

Adult females in mixed groups

Neither the average nor the maximum group sizes of adult females in mixed groups was correlated with mean annual rainfall (Table 4.2; Fig. 4.4). Only maximum group size differed significantly between the two years of high (1971/72) and low rainfall (1982/83), with the median group size being larger in the high rainfall year (Table 4.3; Fig. 4.5). Although the range of group sizes was largest during the low rainfall year, overall, group sizes were larger in the high rainfall year (Fig. 4.5). This indicates that females generally form larger groups when there is higher rainfall and split into smaller groups when there is lower rainfall. In the high rainfall year prey may be more dispersed due to abundant surface water, resulting in a more patchy/ variable availability and leading to the risk-prone behaviour of the lions. In the dry season prey will be in poor condition and therefore more vulnerable to predation.

The average and maximum group sizes of adult females in mixed groups were positively correlated with the variation in rainfall, although only the average group size result was significantly correlated with rainfall (Table 4.4; Fig. 4.6). As with the adult males in mixed groups, the value of the Spearman's correlation coefficient was positive but low for the average group size variable, therefore indicating a slight increase in average adult female group size with increasing rainfall variability (Fig. 4.6). Adult females may form larger groups in order to increase their hunting efficiency in more variable habitats, a risk-prone behaviour pattern. The categorical analyses were significant when based on both variability region area and road coverage (Table 4.5), with the same trend appearing as for both male groupings. More sightings than expected were recorded in the areas of low variability (low: 24-25%; Fig. 4.7) and higher variability (high: 30-33%; Fig. 4.7).

Exclusively adult female groups

Neither the average nor maximum exclusively adult female group sizes were correlated with mean annual rainfall (Table 4.2; Fig. 4.4). The group size of exclusively adult females did not differ significantly between the years of high (1971/72) and low rainfall (1982/83)(Table 4.3). In both years, the median group size was three, while most groups ranged between one and five in size (Fig. 4.5).

Significant positive correlations were found between the variation in rainfall and the average and maximum group sizes of exclusively adult female groups (Table 4.4; Fig. 4.6). The correlation coefficient values were greater for this group than those found for the other lion variables, indicating a slightly greater increase in exclusively adult female group size with increasing rainfall variability (Fig. 4.6). As for the adult females in mixed groups, larger groups may form where conditions are more variable in order to increase hunting success and thus, survival. The categorical analyses were significant when based on both the area of the variability regions and the road coverage (Table 4.5). The same trend appeared as above, i.e., more sightings than expected were recorded in the areas of low variability (low: 24-25%; Fig. 4.7) and higher variability (high: 30-33%; Fig. 4.7).

Subadults

The average and maximum subadult group sizes were not significantly correlated with mean annual rainfall (Table 4.2; Fig. 4.4). Subadult group size did not differ significantly between the two years of high (1971/72) and low (1982/83) rainfall, a median group size of three being recorded for both (Table 4.3; Fig. 4.5). There may be other factors influencing subadult group size, such as cub survival or the number of individuals present in a group at the time of eviction from the pride.

The correlations between rainfall variability and the average and minimum subadult group sizes were positive, but the relationships were not significant (Table 4.4; Fig. 4.6). The categorical analyses based on both the areas and road coverage of the rainfall variability regions were significant (Table 4.5), with more subadult sightings than expected recorded in the areas of higher variability (high: 30-33%; Fig. 4.7). Once again, this may be a result of these areas being patrolled by staff more regularly as they fall along the KNP borders or the lions may be more conspicuous in these areas based on the vegetation type.

Cubs

Neither the average nor the maximum cub group sizes were correlated with mean annual rainfall (Table 4.2; Fig. 4.4). The median cub group size was greater in the low (1982/83) than in the high (1971/72) rainfall year, but this difference was not significant (Table 4.3; Fig. 4.5). Cub survival, and hence group size, is mainly influenced by nutrition (Packer & Pusey 1995), therefore suggesting that although rainfall may influence the environment indirectly, it does not have a direct effect on cub group size.

There were no significant correlations found between the variation in rainfall and either of the cub variables (Table 4.4; Fig. 4.6). The categorical analyses based on both the areas and the road coverage of the rainfall variability regions were significant (Table 4.5), with more cub sightings than expected recorded in the areas of higher variability (high: 30-33%; Fig. 4.7). However, this may be artefact of the data collection method, as the more variable regions lie along the KNP borders (Fig. 4.3), which are patrolled more regularly than the central areas.

Cub: adult female ratio

Reproductive output did not differ significantly with mean annual rainfall (Table 4.2; Fig. 4.4). However, it did differ significantly between the years of low (1982/83) and high (1971/72) rainfall (Table 4.3), being greatest in the year of lowest rainfall (Fig. 4.5). There were therefore more cubs per adult female in the drier year. This may have been a result of cubs being more visible during the dry year when vegetation might have been less dense.

Although a positive correlation was found between the variability in rainfall and the maximum cub to maximum adult female ratio, this relationship was not significant (Table 4.4), suggesting that there is little effect of rainfall variability on reproductive output (Fig. 4.6).

Total group size

Neither the average nor the maximum total group size was correlated with mean annual rainfall (Table 4.2; Fig. 4.4). The averaged maximum total group size was significantly greater in the high rainfall year (1971/72) than in the low rainfall year (1982/83)(Table 4.3; Fig. 4.5). I expected group sizes to be greater when rainfall was high because prey would be more dispersed, therefore the lions are acting in a risk-prone manner as I predicted.

The correlations between rainfall variability and the average and maximum total group sizes were significant and positive (Table 4.4). There is a slight increase in the total group size with

increasing rainfall variability (Fig. 4.6) which suggests that the lions are risk-prone, forming larger groups where conditions are more variable. A significant difference was found in the number of sightings recorded in the three rainfall variability categories based on both the areas and the road coverage of the rainfall regions (Table 4.5). There were more sightings recorded in the low variability (low: 24-25%; Fig. 4.4) and the higher variability regions (high: 30-33%; Fig. 4.7) than expected. Once again, this may be a result of the areas being patrolled by staff more often, or as a result of better visibility in these areas.

Table 4.2. Although rainfall is generally known to have indirect effects on mammal population dynamics, I tested whether mean annual rainfall directly influenced lion group dynamics by running a correlation analysis.

		Average group size		Maximum group size		Ratio	
Lion variable	N [1]	r_s [2]	P	r_s [2]	P	r_s [2]	P
Adult males in mixed groups [a]	1647	-0.017	ns	0.018	ns		
Exclusively adult male groups [a]	1302	0.01	ns	0.05	0.07		
Adult females in mixed groups [b]	1683	-0.027	ns	-0.003	ns		
Exclusively adult female groups [b]	779	-0.064	0.072	-0.071	0.049		
Subadult group size [c]	1078	0.015	ns	0.021	ns		
Cub group size [d]	839	0.019	ns	0.012	ns		
Cub: maximum adult female ratio [e]	826					-0.041	ns
Total group size [f]	1966	-0.016	ns	-0.003	ns		

[1] N = sample size

[2] r_s = Spearman correlation coefficient

Note: The significance levels have been adjusted as the data were used in multiple tests (Schork & Remington 2000). The adjusted critical P values are: [a] P = 0.008; [b] P = 0.007; [c] P = 0.013; [d] P = 0.01; [e] P = 0.006; [f] P = 0.003

Results where P >0.1 have been noted as ns (non-significant), although only results with P< critical level have been interpreted as significant.

Table 4.3. Short-term rainfall may influence lion group dynamics. I tested whether group size differed between two years of extremely high and low rainfall using a Kruskal-Wallis one-way ANOVA.

		Average group size		Maximum group size		Ratio	
Lion variable	N [1]	χ^2	P	χ^2	P	χ^2	P
Adult males in mixed groups [a]	672	20.90	<0.001	35.65	<0.001		
Exclusively adult male groups [a]	450	4.93	0.026	1.45	ns		
Adult females in mixed groups [b]	713	1.53	ns	15.59	<0.001		
Exclusively adult female groups [b]	152	0.06	ns	0.02	ns		
Subadult group size [c]	281	0.31	ns	0.71	ns		
Cub group size [d]	193	2.27	ns	0.14	ns		
Cub: maximum adult female ratio [e]						6.15	0.013
Total group size [f]	966	0.04	ns	10.27	0.001		

Df = 1 in all cases.

[1] N = sample size

Note: The significance levels have been adjusted as the data were used in multiple tests (Schork & Remington 2000). The adjusted critical P values are: [a] P = 0.008; [b] P = 0.007; [c] P = 0.013; [d] P = 0.01; [e] P = 0.006; [f] P = 0.003

Results where P >0.1 have been noted as ns (non-significant), although only results with P< critical level have been interpreted as significant.

Table 4.4. Rainfall variability may affect lion social ecology. Using variation in rainfall as a measure of environmental variability, I tested for correlations between the lion variables and the rainfall coefficient of variation.

		Average group size		Maximum group size		Ratio	
Lion variable	N [1]	r_s^2	P	r_s^2	P	r_s^2	P
Adult males in mixed groups [a]	1647	0.084	0.001	0.046	0.061		
Exclusively adult male groups [a]	1302	0.071	0.011	0.037	ns		
Adult females in mixed groups [b]	1683	0.084	< 0.001	0.059	0.016		
Exclusively adult female groups [b]	779	0.206	< 0.001	0.211	< 0.001		
Subadult group size [c]	1078	0.051	0.093	0.056	0.067		
Cub group size [d]	839	0.029	ns	0.042	ns		
Cub: maximum adult female ratio [e]	826					0.005	ns
Total group size [f]	1966	0.106	< 0.001	0.08	< 0.001		

[1] N = sample size

[2] r_s = Spearman correlation coefficient

Note: The significance levels have been adjusted as the data were used in multiple tests (Schork & Remington 2000). The adjusted critical P values are: [a] P = 0.008; [b] P = 0.007; [c] P = 0.013; [d] P = 0.01; [e] P = 0.006; [f] P = 0.003

Results where P >0.1 have been noted as ns (non-significant), although only results with P< critical level have been interpreted as significant.

Table 4.5. I contrasted the number of observations among the three rainfall variability regions of KNP (Fig. 4.3). The categorical results were all significant, with more sightings than expected recorded for all variables in the areas of higher rainfall variability. There were also more sightings than expected recorded in the areas of low variability for both male and both female group-related sightings.

	Region area		Road area	
Variable	G	P	G	P
Adult males in mixed groups [a]	4386.9	0.001	2299.1	0.001
Exclusively adult male groups [a]	1035.1	0.001	438.8	0.001
Adult females in mixed groups [a]	4415.8	0.001	2271.0	0.001
Exclusively adult female groups [a]	322.4	0.001	153.7	0.001
Subadult group size [b]	518.5	0.001	347.7	0.001
Cub group size [b]	371.6	0.001	268.7	0.001
Total group size [c]	6005.7	0.001	2894.5	0.001

Df = 2 in all cases.

Note: Region area = total area covered by each rainfall variation category

Road area = area covered by road in each rainfall variation category

The critical significance levels have been adjusted as the data were used in multiple tests (Schork & Remington 2000). The adjusted critical P values are: [a] P = 0.008; [b] P = 0.013; [c] P = 0.004

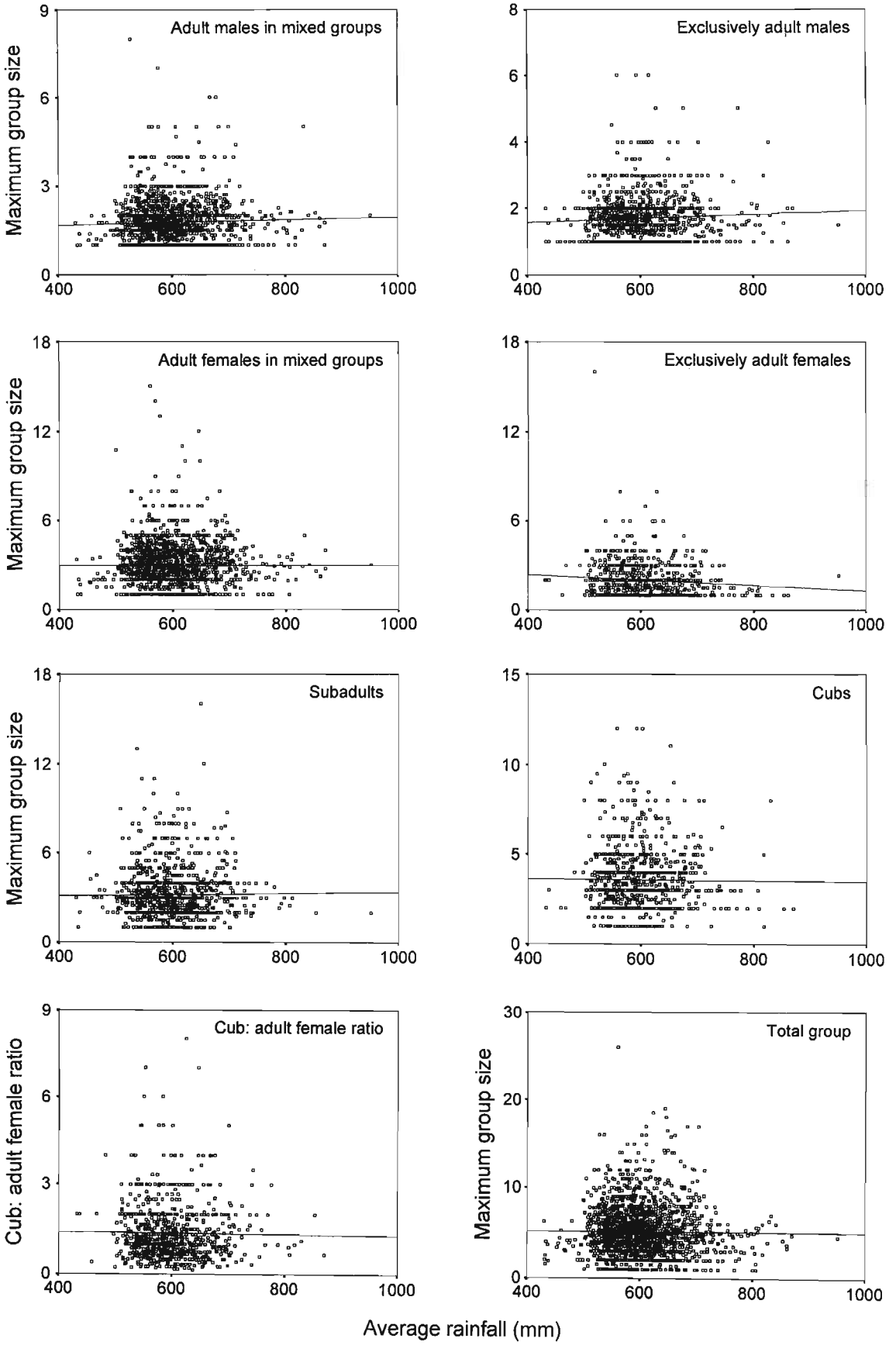

Figure 4.4. Rainfall has been found to influence population dynamics indirectly rather than directly. The scatter plots show that the relationship between lion group sizes does not differ greatly with increasing rainfall across KNP.

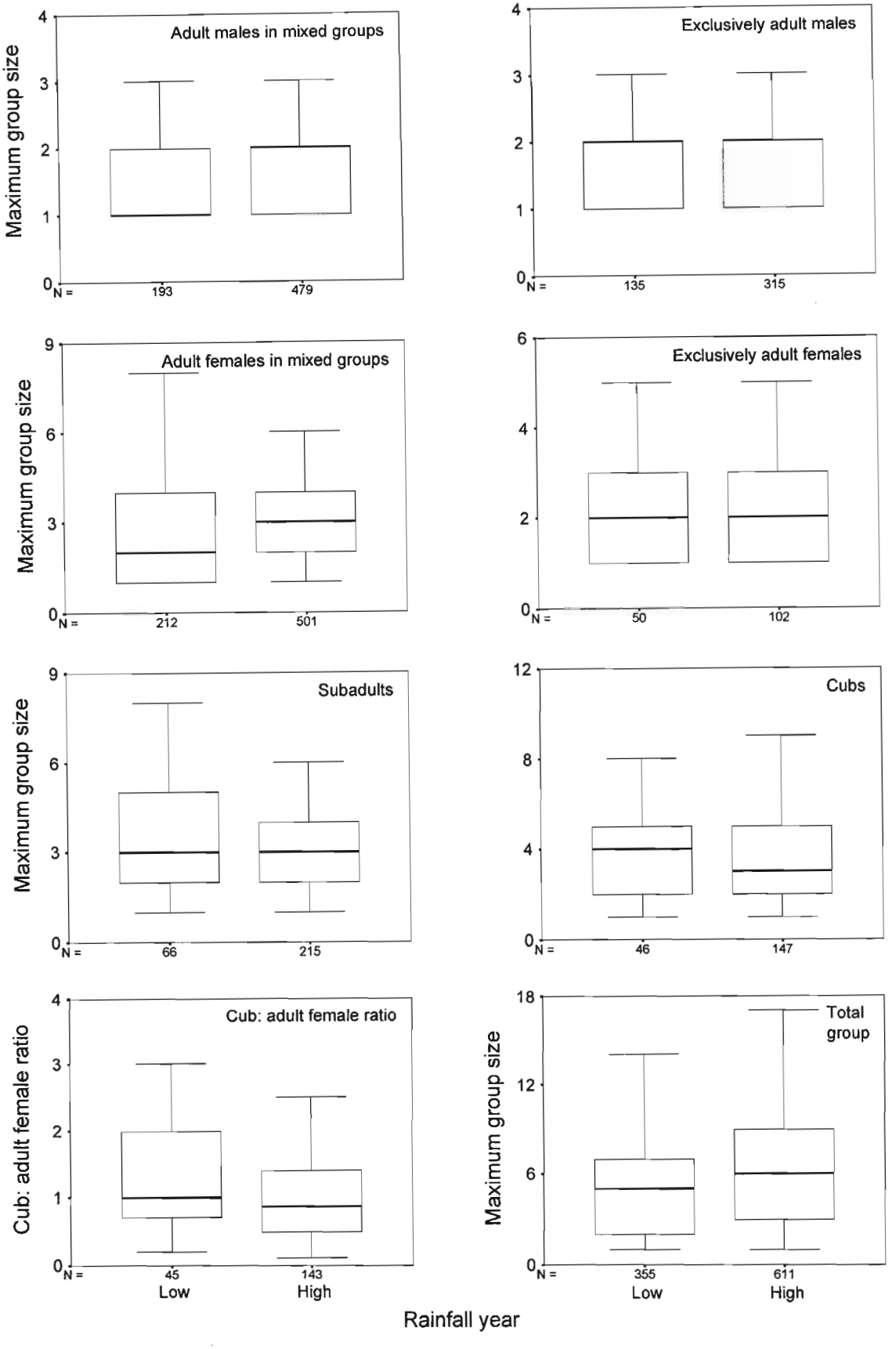

Figure 4.5. Lion group sizes varied between the low and the high rainfall years. The box plots show the median, first and third quartiles and the range. Although, outliers and extremes were used in the analyses I have not represented them in the box plots in order to avoid cluttering and to facilitate interpretation of trends. N = sample size.

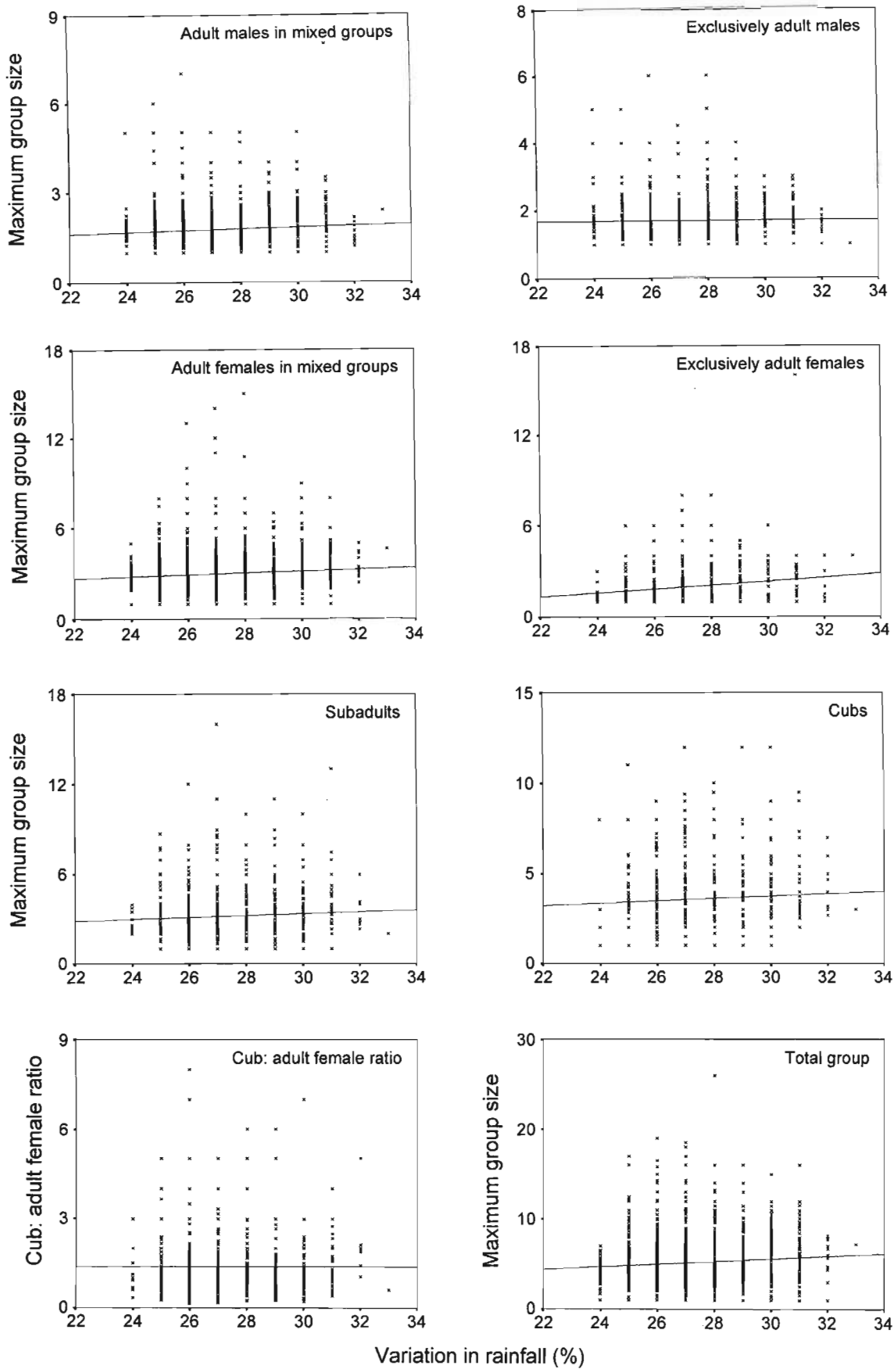

Figure 4.6. Rainfall variability was found to affect certain lion variable group sizes. Where variability had a significant effect, there was a trend for group sizes to increase with increasing rainfall variability.

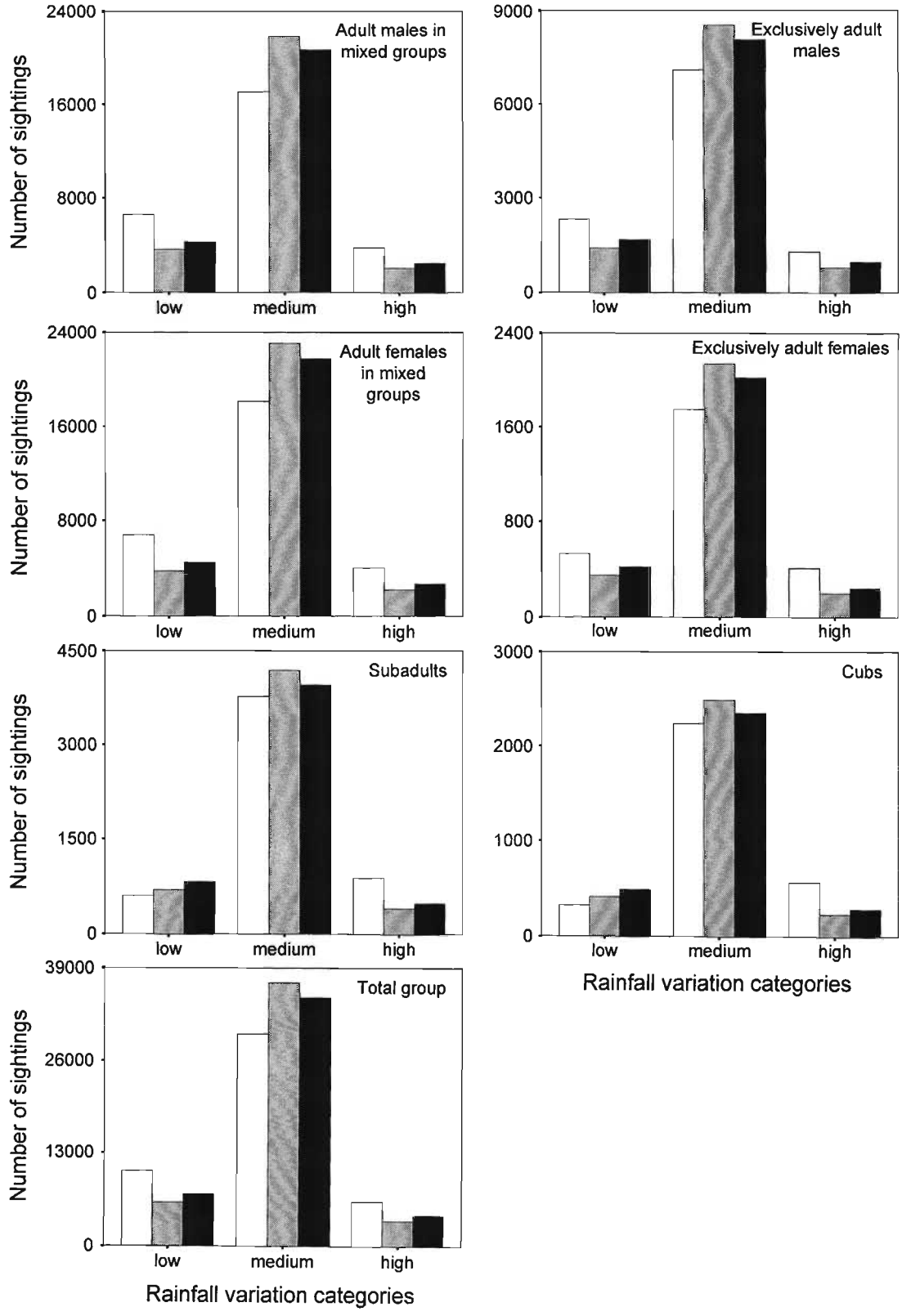

Figure 4.7. The observed number of lion sightings differed between the three rainfall variability categories (low = 24 - 25%; medium = 26 - 29%; high = 30 - 33%). The bar graphs represent the observed number of sightings (open bar) and the expected number based on the area of the variability regions (hatched bar) and the road coverage in each category (shaded bar).

The effect of season on lion group dynamics

There were no significant differences between the averaged average or averaged maximum for any of the lion variable group sizes recorded in the wet and dry seasons (Table 4.6). I have summarised the distribution of the seasonal group sizes for each variable.

Table 4.6. Season could influence group size as a result of changes in prey availability. I tested whether season influenced group size using a Kruskal-Wallis one-way ANOVA. However, the results were not significant for any of the variables.

		Average		Maximum		Ratio	
Lion variable	N [1]	χ^2	P	χ^2	P	χ^2	P
Adult males in mixed groups [a]	2699	0.029	ns	0.017	ns		
Exclusively adult male groups [a]	2057	0.826	ns	0.107	ns		
Adult females in mixed groups [b]	2759	0.213	ns	0.142	ns		
Exclusively adult female groups [b]	1113	0.180	ns	0.184	ns		
Subadult group size [c]	1618	1.454	ns	1.576	ns		
Cub group size [d]	1199	1.824	ns	1.159	ns		
Cub: maximum adult female ratio [e]	1184					3.792	0.052
Total group size [f]	3272	0.410	ns	1.012	ns		

Df = 1 in all cases.

[1] N = sample size

Note: the significance levels have been adjusted as the data were used in multiple tests (Schork & Remington 2000). The adjusted critical P values are: [a] P = 0.008; [b] P = 0.007; [c] P = 0.013; [d] P = 0.01; [e] P = 0.006; [f] P = 0.003

Results where P >0.1 have been noted as ns (non-significant), although only results with P< critical level have been interpreted as significant.

Adult males in mixed groups

The mean number of adult males occurring in mixed groups was about 1.5 in both the wet and dry seasons (Fig. 4.8). An absolute maximum of eight males was recorded in a mixed group in the dry season and six in the wet season, while in both seasons the absolute minimum was one (Fig. 4.8).

Exclusively adult male groups

In both the wet and dry seasons, the mean number of adult males occurring in exclusively adult male groups was about 1.5 (Fig. 4.8). An absolute maximum of seven males was recorded in a mixed group in both the dry and wet seasons, while the absolute minimum was one in both seasons (Fig. 4.8).

Adult females in mixed groups

The mean number of adult females occurring in mixed groups was two in both the dry and wet season (Fig. 4.8). An absolute maximum of 15 females was recorded in a mixed group in the dry

season and 18 in the wet season. while in both seasons the absolute minimum was one (Fig. 4.8).

Exclusively adult female groups

In both the dry and wet seasons. the mean number of females occurring in an exclusively adult female group was two (Fig. 4.8). An absolute maximum of eight females was recorded in the dry season and 16 in the wet season, while in both seasons the absolute minimum was one (Fig. 4.8).

Subadults

The mean number of subadults was about 2.7 in the dry season and 2.8 in the wet (Fig. 4.8). The absolute maximum number of subadults was 16 and the absolute minimum was one in both the wet and dry seasons (Fig. 4.8).

Cubs

The mean number of cubs recorded in both the wet and dry season was three (Fig. 4.8). An absolute maximum of 16 cubs in the dry and 14 in the wet season were recorded and an absolute minimum of one was recorded in both seasons (Fig. 4.8).

Cub: adult female ratio

Although a P value of 0.052 (Table 4.6) was obtained for the maximum cub to maximum adult female ratio recorded in each season, there was negligible difference between their means, which were both ±1.2 (Fig. 4.8). The absolute maximum cub to adult female ratio (16, Fig. 4.8) recorded in the dry season, might have arisen as a result of one female remaining with the crèche of cubs while the other females hunted. The absolute minimum ratios recorded in both seasons approached zero, indicating a very low cub to adult female ratio and thus a low reproductive output.

Total group size

The mean total group size was about four in both seasons (Fig. 4.8). The absolute maximum group size recorded in the dry season was 32 and the absolute minimum was one. In the wet season the absolute maximum was 26 and the minimum was also one (Fig. 4.8).

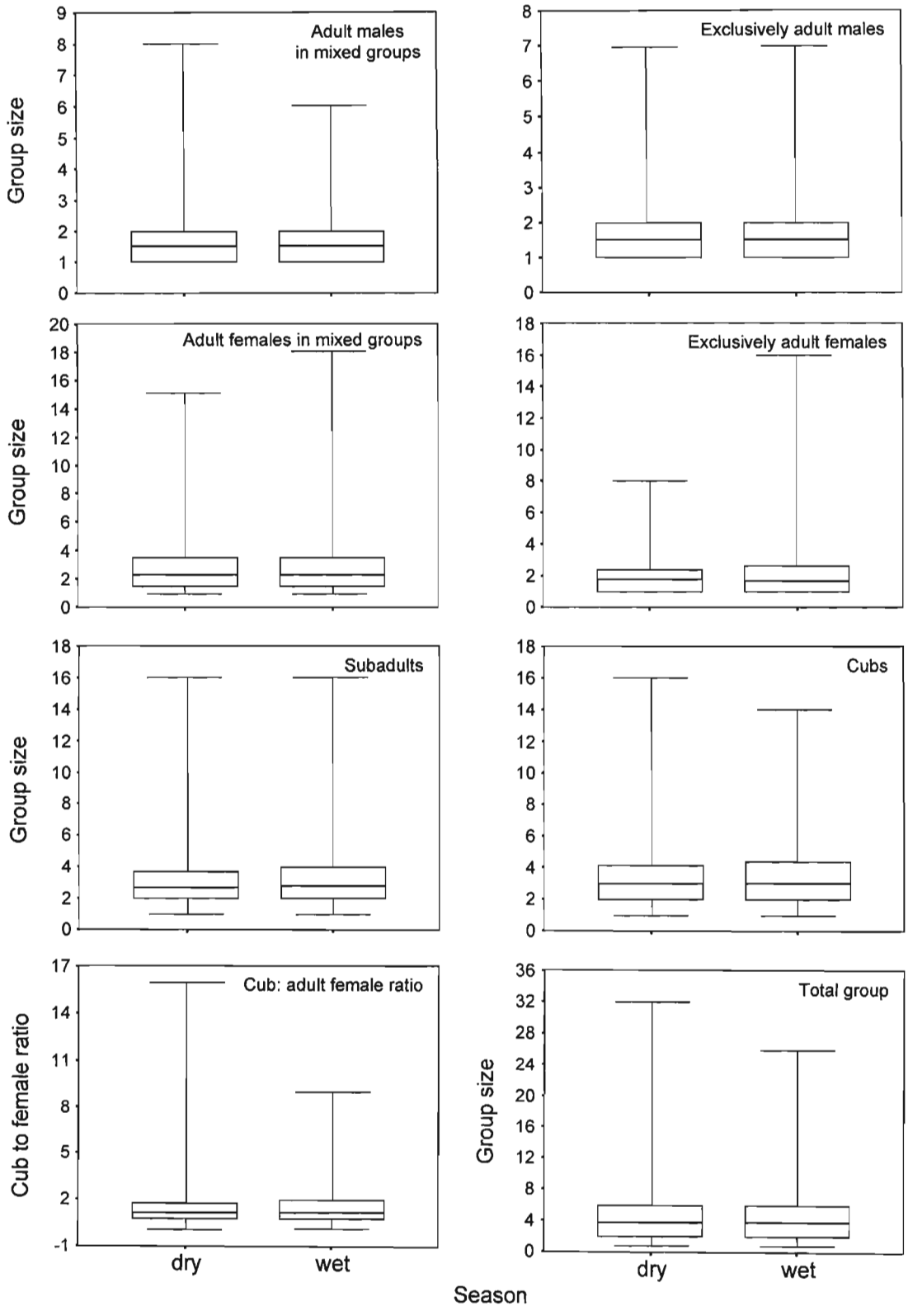

Figure 4.8. Lion group size was compared between the wet and dry seasons. The box-and-whisker plots show the absolute maximum, absolute minimum, mean and the first and third quartiles of the data.

Season as a measure of visibility

The results of the categorical analyses (G test) comparing the total number of sightings recorded for each lion variable in the wet and dry seasons, were all significant except for adult females in exclusively adult female groups (Table 4.7). There were more sightings recorded in the dry season than expected for the other lion variables (Fig. 4.9). During the dry season vegetation appears more open/ less dense due to natural die back or leaf loss, which may result in lions being more visible. As part of this chapter I looked at rainfall season as a measure of visibility. My data upheld my prediction that there would be more sightings during the dry than during the wet season.

Table 4.7. Visibility should differ between the wet and dry seasons as a result of vegetation die back. This should be noted by a difference in the number of sightings recorded in the two seasons. The categorical results (G tests) were all significant except for adult females in exclusively adult female groups, with more sightings than expected recorded in the dry season and less than expected recorded in the wet season.

Lion variable	G	P
Adult males in mixed groups [a]	88.69	0.001
Exclusively adult male groups [a]	10.52	0.01
Adult females in mixed groups [a]	93.56	0.001
Exclusively adult female groups [a]	2.08	0.05
Subadult group size [b]	23.62	0.001
Cub group size [b]	8.66	0.01
Total group size [c]	126.75	0.001

Df = 1 in all cases.

Note: The critical significance levels have been adjusted as the data were used in multiple tests (Schork & Remington 2000). The adjusted critical P values are: [a] P = 0.017; [b] P = 0.025; [c] P = 0.007

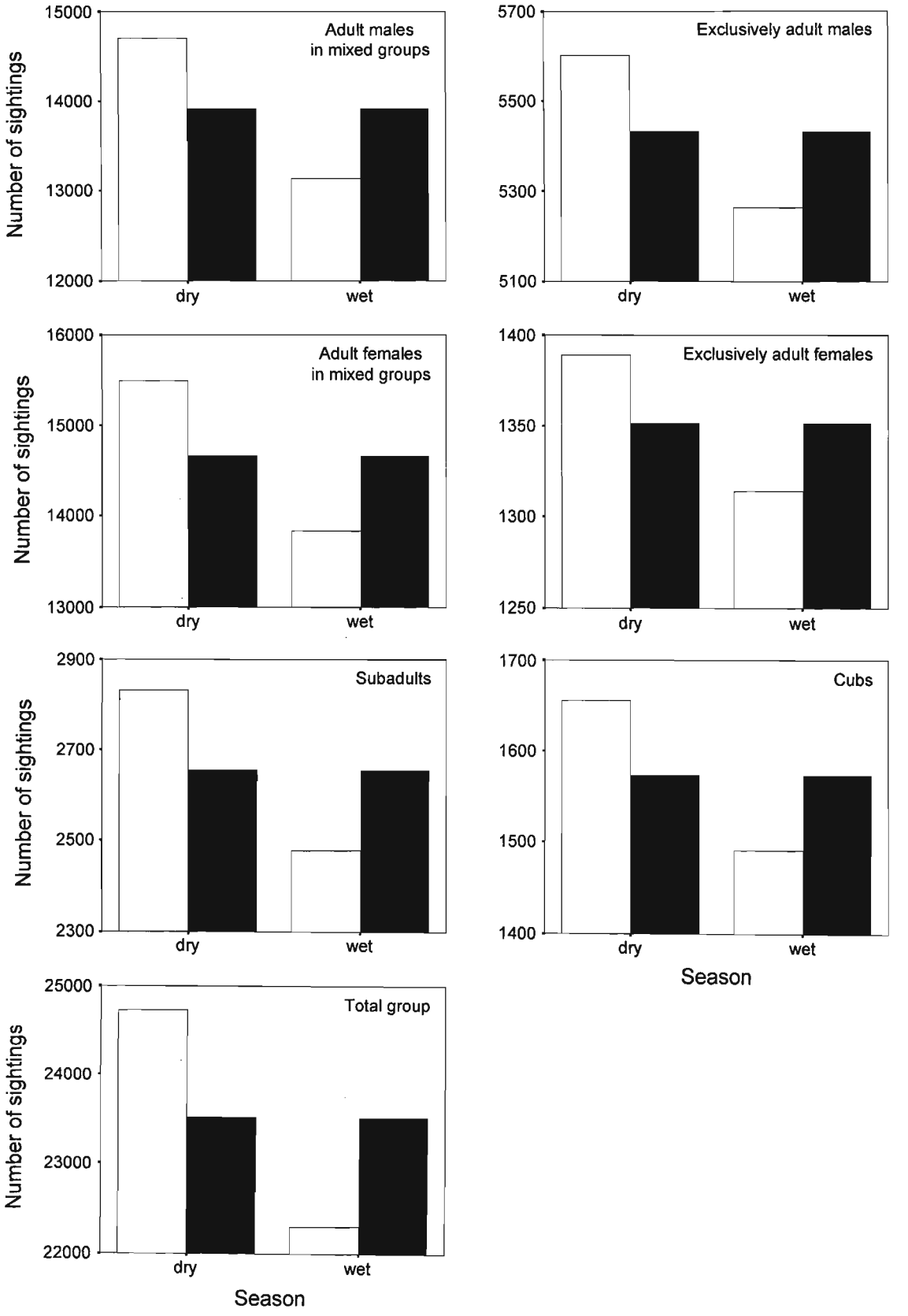

Figure 4.9. The number of observations was contrasted between the wet and dry seasons. The bar graphs represent the number of observed sightings (open bar) and the number of expected sightings (shaded bar) during the dry and wet seasons.

Discussion

Rainfall directly affects habitat quality and structure through its influence on vegetation (De Bie *et al.* 1998; Van Heezik & Seddon 1999). Plant primary productivity affects the carrying capacity of the environment/ habitat in which herbivores occur, thereby influencing their density (Van Rooyen, Bezuidenhout, Theron & Bothma 1990; Fritz & Duncan 1994). This in turn influences the density of predators that can be supported by the environment (Kleiman & Eisenberg 1973; Van Orsdol 1982; Van Orsdol *et al.* 1985; Heinsohn 1997; Stander *et al.* 1997).

While rainfall variability is an important factor, the predictability of rainfall should not be overlooked. Although I have not analysed predictability in this project, it is an important environmental process in savanna ecosystems (Scholes & Walker 1993). Rainfall is not predictable in terms of amount and duration and this has an effect on the plants and animals of this ecosystem (Scholes & Walker 1993).

In terms of social predators, rainfall through its influence on prey density, or abundance, can have an influence on the foraging/ hunting group sizes formed (Stander 1992b) and on predator reproduction (Packer *et al.* 1990). There is an indirect rather than a direct effect of rainfall on predator dynamics through rainfall's influence on the environment and hence the variability of that environment.

Risk-sensitive foraging has been used as a mechanism to explain why group sizes differ between regions. Both Packer *et al.* (1990) and Stander (1992b) found that it was advantageous for lions to form larger groups when prey were scarce during the dry season, while group size was relatively unimportant in terms of fulfilling the lions' daily food requirements when prey were abundant in the wet season. In both cases the lions showed risk-prone behaviour. If the lions were unable to capture a large prey animal, the meal from a small animal would be spread further resulting in more lions not meeting their daily minimum requirements than if they had foraged on their own and caught a smaller animal. Packer *et al.* (1990) determined that in the Serengeti, optimal hunting groups in the dry season and actual group sizes differed significantly. A group size of two to four, although the least advantageous, was the most preferred group size range. Therefore there must be other factors apart from optimal foraging that affect group size, such as cub defence.

Although I found risk-prone behaviour in certain lion groups across variability regions, I did not find it across mean annual rainfall regions or across seasons. As found by Packer *et al.* (1990) in

the dry season, when food supply fluctuates as it would in a variable environment, it is more advantageous for lions to form larger groups to guarantee a meal and thus fulfil their minimum daily requirements. Hunting success has been shown to increase asymptotically with an increase in hunting group size (Schaller 1972; Van Orsdol 1984; Packer & Ruttan 1988) and a larger group also facilitates the capture of larger prey species (Kruuk 1972; Schaller 1972). Therefore the lions in KNP may be exhibiting risk-prone behaviour across regions to ensure that they meet their minimum daily requirements throughout the year.

My data on group size may not have differed significantly on a seasonal basis because, unlike in the Serengeti where the prey migrate, in KNP there are numerous waterholes throughout the park which reduce the need for mass migrations to find water and result in resident prey populations (Smuts 1976). This effect has been noted in numerous reserves where artificial water points have been introduced (Berry 1981; Mills & Retief 1984; Kalikawa 1990; Stander 1991). Therefore, while many prey populations are sedentary in KNP, even if prey break up into smaller groups in the dry season when forage and browse are limited (Dekker, van Rooyen & Bothma 1996), these small groups may still gather over a small area around the waterholes forming large aggregations of prey animals. Many ungulates are water-dependent and consequently will always remain within a certain distance of water (Western 1975; Beardall, Joubert & Retief 1984; Scogings, Theron & Bothma 1990; Hunter 1996) or travel to water daily. In summer, the rainy season, ungulate group sizes tend to increase (Underwood 1982) because the abundance of browse and forage allow for larger group formation. Although hunting may be more difficult in the dry season due to the decrease in cover (Van Orsdol 1984), the variation in prey availability and vulnerability (Mills *et al.* 1995) may not be sufficient to result in noticeable differences in functional group sizes between the wet and dry seasons.

Lions are not known to be seasonal breeders (Schaller 1972). Productivity and the survival rate of cubs varies on a seasonal basis and with variation in rainfall within years as a consequence of changes in prey abundance (Van Orsdol 1982; Packer *et al.* 1988). On the Serengeti plains, Packer & Pusey (1995) found that lion productivity (the number of cubs to survive to one year of age) reached a peak when the migratory herds were abundant on the plains for longer periods during the dry season. Season also affects cub mortality, with mortality being greater in the dry season than in the wet season (Van Orsdol 1982; Hanby *et al.* 1995). Although I found very little difference between the reproductive output of adult females either across rainfall regions, variability regions or seasons, there was a difference between the two years of extreme rainfall. However, opposite to what I predicted, the output was greater in the low rainfall year. Cubs may

have been more visible during the drier year due to vegetation die back. Alternatively, food might have been more abundant due to prey, especially buffalo, being in bad condition.

Foragers may change between risk-averse and risk-prone behaviour depending on their physiological status or daily energy budget (Young *et al.* 1990). For granivorous birds feeding on seeds, it may be better to forage alone when food is variable in order to ensure that when food is found it need not be shared. Alternatively, foraging in a group would increase an individual's probability of finding food and thus of fulfilling its minimum daily requirements (Ekman & Hake 1988). In terms of lions, however, generally one prey animal will be hunted from a herd and shared by group members. In a variable environment, hunting small prey animals may lead to greater energy expenditure than is regained from the meal. Hence, a larger group size may be the risk-prone alternative in a variable environment as the individuals are able to secure a larger prey animal and thus attain a larger meal and fulfil their daily food requirements. This appears to be the case in certain areas where larger groups form in the dry season when prey is scarcer (the environment is more variable; Packer *et al.* 1990; Stander 1992b). My annual data conforms to this idea as total and functional (groups with adult females) group size increased with increasing rainfall variability. However, there were no significant differences in either the total group sizes, or the functional group sizes between seasons. The lack of seasonal prey migrations in KNP and thus periods of major prey scarcity might reduce the necessity for lions to change their group dynamics on a seasonal basis; or as Packer *et al.* (1990) concluded, there might be factors other than foraging optimality which affect group size.

Foraging optimisation, while playing an important role, is not the only factor affecting lion group dynamics and habitat selection. There are numerous social factors that also affect group formation such as territory defence and defence of cubs from infanticidal males (Packer *et al.* 1990; Pusey & Packer 1994). While prey abundance does affect group size (Stander 1992b), rainfall through its influence on the availability of water can affect lion, and especially cub, survival (Hanby *et al.* 1995).

CHAPTER FIVE
LION SPATIAL SOCIO-ECOLOGY – A COMBINATION OF INTERACTING FACTORS

Introduction

There are multiple factors, both biotic and abiotic, that influence population dynamics, such as habitat structure, food and habitat variability (Taylor & Green 1976; Caughley 1977; Gill 1998). All three elements relate to resource availability (mainly food) and can be used to explain why groups form and how they should distribute themselves in order to increase individual fitness. In Chapters Two to Four, I investigated three mechanisms that could be used to explain group formation and distribution, namely ideal free distribution (Chapter Two; Fretwell & Lucas 1970), the resource dispersion hypothesis (Chapter Three; Macdonald 1983) and risk-sensitive foraging (Chapter Four; Stephens & Krebs 1986). However, while each of these mechanisms can be studied separately, out in the field it is a combination of these factors plus many others that will influence group dynamics.

Lions are social, territorial animals that lend themselves to an investigation on why, how and where groups should form. They live in fission-fusion groups (Packer *et al.* 1990), that can change in size according to environmental or social influences and, over time (Van Orsdol *et al.* 1985; Stander 1997). Although food availability in an area is an important determinant of group size and territory size (Van Orsdol *et al.* 1985; Stander 1997), the habitat structure determines how the area is utilised (Van Orsdol 1984). Therefore it is a combination of these factors that will determine where the lions are distributed and their group sizes. While other factors, such as cub and territory defence (Packer *et al.* 1990), are also crucial elements in determining group dynamics, resource availability and habitat structure and quality should be useful for deriving explanations of group dynamics under certain conditions.

Environmental patterns and processes do not act in isolation. Therefore the aim of this chapter was to determine which factors, and/ or combinations thereof, acted to influence lion group dynamics. Although I found group size distribution to be similar across seasons (Chapter Four), I decided to look at specific lion variables separately for the wet and dry seasons to determine if the same factors were influencing group dynamics across seasons. I expected the determinants of group size to differ between seasons, with rainfall variability being more important in the dry than in the wet season. I also expected male and female lions to be influenced by different prey combinations as their favoured prey species differ (Rudnai 1974; Scheel 1993; Funston *et al.*

1998). I expected cubs to be influenced by prey and habitat variability in the dry season. If habitat structure were influential, I would expect it to be important in both seasons.

Methods

The effect of biotic and abiotic factors on lion group dynamics

To determine which factors investigated in the previous chapters influenced group dynamics, I ran log-linear analyses including only those variables from the previous chapters that had resulted in significant differences between group sizes. These included habitat structure, individual prey abundance and the coefficient of variation in rainfall.

I worked with the lion data from 1978 to 1985 in two sets, the dry season data (April to September) and, the wet season data (October to March). I only used the data from 1978 as this corresponds to the first year when full aerial censuses were carried out (Chapter Three) and stopped with the data in 1985, as this was the year when the monthly predator returns were stopped (Chapter One). I used the maximum lion data for total adult group size, exclusively adult male groups, exclusively adult female groups, and cubs from 1978 to 1985. These data were averaged per cell for the eight-year period used in the dry season analyses (April 1978 – September 1985) and for the seven-year period used in the wet season analyses (October 1978 – March 1985). Details of the lion data are presented in Chapter One. In order to run log-linear analysis (see below), the data had to be categorical (Knoke & Burke 1980). I therefore separated the group sizes of the four lion variables into categories. Total adult lions were divided into four categories, namely (1) solitary individuals, (2) groups of two (3) groups of three to four and (4) groups of five to 30 (Table 5.1). Preliminary analyses showed that dividing the exclusively adult male and female groups into three categories resulted in very few counts with an increase in the number of variables used in the log-linear models. Thus I separated both adult groups into two categories, (1) those of solitary individuals only and (2) those of two and above (Table 5.1). For cubs I used (1) groups of one and two, (2) three and four and (3) five and above (Table 5.1).

I included only those prey species that had a significant effect on group size in Chapter Three, namely, buffalo, impala, wildebeest and zebra. In Chapter Three, I found buffalo abundance to be important to exclusively adult male groups and to exclusively adult female groups. Adult females in mixed groups were correlated with impala while adult males in mixed groups were correlated with wildebeest. Previous studies have found impala to be important to both males and females while wildebeest are generally associated with adult females (Rudnai 1974; Scheel 1993; Funston *et al.* 1998).

I used the same prey abundance data produced in Chapter Three for both seasons' analyses. Although the prey abundance data were determined for the dry season, the presence of

numerous waterholes throughout KNP has reduced the need for animals to migrate (Pienaar 1985). This should result in minimal differences between the prey distributions between seasons. As I worked with categorical data, i.e. levels of prey abundance, not actual numbers, there should be minimal effects on the results. I determined the prey abundance categories by assigning the values for each prey species from the entire park into size categories such that each category was approximately equal in size. For example, where four size categories were used, each was approximately made up of one quarter of the total number of cells available.

I used two sets of categories for buffalo, impala and wildebeest depending on the lion variable studied because for certain models, the combination of variables resulted in very low cell counts for specific categories or combined categories. For example, when I ran a preliminary log-linear analysis for cubs in the dry season using buffalo with four categories, the cell counts were very low for all three cub group size categories in the fourth buffalo category. The cross-tabulation table showing the cell counts for cubs for the two-way interaction between buffalo and impala abundance resulted in none or only one cell occurring where the categories of buffalo and impala abundance were both four. I therefore used two different prey category data sets for certain analyses as the few sightings at the higher category level clouded analysis and interpretation of the results (Table 5.1). I used four categories of buffalo abundance for exclusively adult male groups (buffalo [1], Table 5.1). I used three categories of buffalo abundance (buffalo [2]) for the models involving the total adult group size and exclusively adult female groups (Table 5.1). In the exclusively adult male model I also used impala abundance with four categories (impala [1], Table 5.1) while I used three impala abundance categories for the cub analyses (impala [2], Table 5.1). I also separated wildebeest abundance into two category sets, using the three category data (wildebeest [1], Table 5.1) in the exclusively adult female group analyses and the two category data for the cub analyses (wildebeest [2], Table 5.1). I divided zebra abundance into two categories only, either low (less than 11, Table 5.1) or high (more than 11 individuals, Table 5.1).

I used the annual coefficient of variation in rainfall calculated in Chapter Four for both seasons, as this is an overall long-term effect that will affect habitat variability throughout the year. I used the same three categories of variation that I used in the Chapter Four analyses, namely low, medium and high (Table 5.1).

I used the same habitat definitions for both seasons as used in Chapter Two, ranging from dense vegetation (thickets) to more open vegetation (open tree savanna).

Table 5.1. The variables used in the log-linear analyses included four lion variables, four prey species, the coefficient of variation in rainfall and habitat structure. As log-linear analysis requires categorical data I have reclassified the continuous variables into categories.

		Categories			
Variables	Codes	Very low	Low	Medium	High
Total adult group size	T	1	2	3-4	5-30
Exclusively adult males	M		1		2-6
Exclusively adult females	F		1		2-30
Cubs	C		1-2	3-4	5-16
Rainfall coefficient of variation (%)	V		24-25	26-29	30-33
Buffalo (1)	B	1-14	15-49	50-124	125-752
Buffalo (2)	B_2		1-20	21-80	81-752
Impala (1)	I	12-29	30-35	36-45	46-124
Impala (2)	I_2		12-30	31-40	41-124
Wildebeest (1)	W		3-8	9-11	12-56
Wildebeest (2)	W_2		3-10		11-56
Zebra	Z		5-11		12-52
Habitat	H	Thickets	Woodlands	Mountainous	Open tree savanna

Note: See text for explanation of variables and categories.

I used log-linear analysis in place of MANOVA, as the data were not normally distributed even when transformed (Kolmogorov-Smirnov, $P < 0.05$). Log-linear analysis is essentially a multiple G-test that allows for the simultaneous contrast of the effects of a number of categorical variables on each other. To analyse my data I set up logit models, which allow one variable to be set as the dependent variable (Knoke & Burke 1980), in this case the respective lion variables. The remaining variables (habitat structure, prey species and coefficient of variation in rainfall) are interpreted as independent variables, between which interaction effects can also be determined (Knoke & Burke 1980).

The process involved constructing a baseline model with all the independent effects on each other included, and then adding in the dependent variable. In the results section I refer to this as the 'no independent effects' model. The interaction of each independent variable with the dependent variable is then added to this model. The change in L^2 (the log-likelihood ratio) of the new model relative to the baseline model gives the strength of the effect of that independent variable. The log-likelihood ratio compares the expected with the observed count frequencies (Knoke & Burke 1980). The change in L^2 (ΔL^2) is tested for statistical significance at the change in degrees of freedom (Δd.f.). The change in degrees of freedom is the difference between the degrees of freedom of the baseline model and the alternative model.

I set up a new baseline model that took into account the effects of each independent variable on the dependent variable in order to determine two-way interaction terms. In the results section I

refer to this model as the baseline model. From this model, the effect of interaction terms on the dependent variable could be determined.

To determine the amount of variance that is described by the significant variables in each of the models produced, Q^2 can be calculated. Q^2 is an analog to the coefficient of determination (R^2) for multiple regression (Knoke & Burke 1980; Bakeman, Forthman & Perkins 1992). It is calculated using the log-likelihood ratio (L^2) of the baseline and alternative models as follows (Bakeman *et al.* 1992):

Q^2 = (L^2 for the baseline model - L^2 for the alternative model) / L^2 for the baseline model

I ran each lion variable with those factors that I had found important in previous chapters and those that other authors have found to influence lion group dynamics. For each lion variable, I used the same initial models for the wet and dry season analyses to determine if there were seasonal changes in the effects that prey and habitat had on lion group dynamics. I used coefficient of variation in rainfall and habitat in all analyses, buffalo (2) and zebra for total adult groups, buffalo (1) and impala (1) for adult males, buffalo (2) and wildebeest (1) for adult females, and wildebeest (2) and impala (2) for cubs.

Bar graphs of the actual data have been used to illustrate the results of the log-linear analyses.

Spatial patterns

I created continuous surface maps in Arcview for each of the four lion variables using the final wet season and final dry season averaged maximum group size data for each variable. I compared the distribution of the group sizes against the surface maps of the independent variables that had a significant effect on group size, to determine whether the patterns of distribution varied across KNP. I created a combined map of the lion variable maps with the independent variable maps for the one-way interactions only. I did not create combination maps for the two-way interaction terms because the resultant maps consisted of too many categories, which would not aid interpretation of the results.

Results

The effect of biotic and abiotic factors on lion group dynamics

Total adult group size

The influence of prey, habitat structure and rainfall variability on adult lion group dynamics differed on a seasonal basis. In the dry season, total adult group size was influenced by buffalo abundance (Table 5.2). There was a decrease in solitary individuals and groups of two and an increase in the groups of five and above with an increase in buffalo abundance (Fig. 5.1). Groups of three to four adults were evenly spread in all areas of buffalo abundance during the dry season (Fig. 5.1). During the wet season, there were a number of factors influencing adult lion group dynamics (Table 5.2). First, buffalo abundance alone had an effect, with an increase in the groups of two adults, three to four adults and, five and above adults with increased buffalo abundance, while solitary individuals decreased. There was a more definite pattern of increased occurrence of large groups with increased buffalo abundance and decreased solitary individuals and groups of two, in the dry season than in the wet season (Fig. 5.1). Solitary adults are unable to hunt buffalo, therefore their distribution will be influenced by other prey and habitat factors. The occurrence of groups of adults as a whole was generally greater at higher buffalo abundance (Fig. 5.1).

Total adult groups were also influenced by the interaction between the coefficient of variation in rainfall and buffalo abundance and that between habitat and zebra abundance during the wet season (Table 5.2). Overall, all four adult categories peaked in number at medium rainfall variation levels (26-29%) regardless of buffalo abundance (Fig. 5.1). In areas of high variation (30-33%), the number of observations of solitary individuals decreased with increasing buffalo abundance, while the three adult group categories increased with increasing buffalo abundance (Fig. 5.1). In areas of low variation in rainfall (24-25%), there were more solitary individuals and groups of five to 30 adults at low buffalo abundance and an increasing number of groups of two, and three to four, at higher buffalo abundance (Fig. 5.1). As found in Chapter Four, it may be more beneficial for lions to form larger groups in more variable environments as it would enable them to hunt larger prey such as buffalo and thereby fulfil their daily food requirements. In areas of low rainfall variation, all individuals, regardless of group size, should be able to attain their daily food requirements.

In terms of habitat structure and zebra abundance, at levels of both low and high zebra abundance, all groups were at a maximum in the open tree savanna and second highest in the woodlands (Fig. 5.1). Zebra are grazers and are therefore naturally associated with the open tree

savanna areas. Although they have also been found to be associated with high tree canopy cover (Page & Walker 1978; Dekker *et al.* 1996). The fact that the same pattern of habitat preference appears for the groups of adults in areas of both low and high zebra abundance, may indicate that lions are selecting these areas because of the associated availability of zebra.

Table 5.2. The influence of biotic and abiotic factors on adult lion group dynamics changes on a seasonal basis. In both seasons coefficient of variation (V), habitat (H), buffalo (2)(B_2) and zebra (2)(Z), were set as independent variables and the dependent variable as total adult group size (T). I have only presented significant interactions.

Effect	Model	L^2 [a]	ΔL^2 [b]	d.f.[c]	P[d]	Q^2 (%)[e]
Dry season						
No effects	[ ]	940.23		287		
No independent effects	[VHB_2Z] [T]	187.52		213		
Buffalo abundance[f]	[VHB_2Z] [TB_2]		20.20	6	0.002	10.8
Wet season						
No effects	[ ]	813.52		287		
No independent effects	[VHB_2Z] [T]	188.23		213		
Buffalo abundance[f]	[VHB_2Z] [TB_2]		15.14	6	0.019	8.0
Baseline[g]	[VHB_2Z] [TV] [TH] [TB_2] [TZ]	157.13		189		
Coefficient of variation * Buffalo[h]	[VHB_2Z] [TH] [TZ] [TVB_2]		22.77	12	0.03	14.5
Habitat * Zebra[i]	[VHB_2Z] [TV] [TB_2] [THZ]		18.59	9	0.029	11.8

[a] L^2 = log-likelihood ratio
[b] ΔL^2 is the change in the log-likelihood ratio
[c] d.f.: where L^2 has been presented, d.f. is the degrees of freedom for the model, where ΔL^2 has been presented, d.f. is the change in degrees of freedom caused by the effect(s).
[d] P = the significance of the variable's effect.
[e] Q^2 is an R^2 analog that describes the amount of variation explained by the interaction terms that is not explained by the baseline model.
[f] The effect of buffalo abundance on total adult group size.
[g] The model incorporating all single order independent term effects.
[h] Model that describes the interaction of coefficient of variation in rainfall and buffalo effects on total adult group size.
[i] Model that describes the interaction of habitat structure and zebra abundance effects on total adult group size.
Note: B_2 is the buffalo abundance based on three abundance categories (Table 5.1).

Exclusively adult males

In the dry season, there was a significant relationship between the exclusively adult male groups and the coefficient of variation in rainfall (Table 5.3). There were a larger number of single males in areas of higher variation and more groups of males at lower variation (Fig. 5.2). At the two-way interaction level, impala and buffalo were acting together to influence adult males (Table 5.3). Males on their own were predominant in areas of higher impala abundance and very low to medium buffalo abundance while groups of males were present to a larger degree in areas of both medium to high impala and buffalo abundance (Fig. 5.2). In the wet season, impala on their own significantly influenced adult male groups, with more single males than coalitions in areas of low to high abundance (Table 5.3). At very low impala abundance there were more groups than solitary males, which may indicate a change in prey preference at low

impala abundance that requires larger groups (Fig. 5.2). At the two-way interaction level, habitat and coefficient of variation in rainfall acted together to influence adult males (Table 5.3). There were more solitary males and groups of males in areas of medium variation in two habitats, the thickets and open tree savanna (Fig. 5.2). In the dry season, variation in rainfall is important on its own, while during the wet season, it is the interaction of rainfall variation with habitat structure that has an effect on adult males. During the dry season when water is less abundant, rainfall variability will have an effect on adult male lions, as the variability of the environment will influence prey availability.

Table 5.3. The influence of biotic and abiotic factors on adult male lion group dynamics changes on a seasonal basis. The log-linear results show two separate one-way and one two-way interaction that influence adult male lions in the wet and dry seasons. In both seasons buffalo (1)(B), impala (1)(I), habitat (H) and coefficient of variation (V) were set as independent variables and the dependent variable as adult male group size (M). I have only presented significant interactions.

Effect	Model	L^2 [a]	ΔL^2 [b]	d.f.[c]	P[d]	Q^2 (%)[e]
Dry season						
No effects	[ ]	834.67		383		
No independent effects	[BIHV] [M]	171.53		191		
Coefficient of variation[f]	[BIHV] [MV]		13.15	2	0.001	7.7
Baseline[g]	[BIHV] [MB] [MI] [MH] [MV]	149.34		180		
Buffalo * Impala[h]	[BIHV] [MH] [MV] [MBI]		18.84	9	0.027	12.6
Wet season						
No effects	[ ]	695.34		383		
No independent effects	[BIHV] [M]	148.15		191		
Impala[i]	[BIHV] [MI]		9.70	3	0.021	6.6
Baseline[g]	[BIHV] [MB] [MI] [MH] [MV]	129.82		180		
Habitat * Coefficient of variation[j]	[BIHV] [MB] [MI] [MHV]		14.57	6	0.024	11.2

[a] L^2 = log-likelihood ratio
[b] ΔL^2 is the change in the log-likelihood ratio
[c] d.f.: where L^2 has been presented d.f. is the degrees of freedom for the model, where ΔL^2 has been presented d.f. is the change in degrees of freedom caused by the effect(s).
[d] P = the significance of the variable's effect.
[e] Q^2 is an R^2 analog that describes the amount of variation explained by the interaction terms that is not explained by the baseline model.
[f] The effect of coefficient of variation on exclusively adult male groups.
[g] The model incorporating all single order independent term effects.
[h] Model that describes the interaction of buffalo and impala effects on exclusively adult male groups.
[i] The effect of impala abundance on exclusively adult male groups.
[j] Model that describes the interaction of habitat and coefficient of variation effects on exclusively adult male groups.

Exclusively adult females

In the dry season, there were no direct effects between the variables tested and adult female groups. At the two-way interaction level, wildebeest and buffalo acted together to influence adult females (Table 5.4). Females on their own were predominant in areas of medium to high wildebeest abundance, when buffalo were in low to medium abundance, while groups of

females were present in areas where buffalo abundance ranged from low to high and wildebeest were in high abundance (Fig. 5.3). In the wet season, there were two significant one-way interactions (Table 5.4). The coefficient of variation in rainfall however, explained more of the variance in the model than buffalo abundance (Table 5.4). The coefficient of variation in rainfall significantly influenced adult female groups, with more groups of females than solitary females in areas of medium to high variation (Table 5.4; Fig. 5.3). There were more groups of females than solitary females in areas of medium to high buffalo abundance (Fig. 5.3). Solitary adult females are unable to capture buffalo on their own, therefore, other variables, such as small prey distribution and the presence of other female lions, will be driving their distribution. At the two-way interaction level, wildebeest and buffalo abundance together influenced adult females (Table 5.4). There were more solitary females in areas of low buffalo abundance, where wildebeest were in medium to high abundance, and more groups of females in areas of medium buffalo abundance and high wildebeest abundance (Fig. 5.3). Wildebeest have been reported to be important prey of adult females (Rudnai 1974; Scheel 1993; Funston *et al.* 1998), while larger groups of females will also be able to capture buffalo. These models predict that variation in rainfall is only important during the wet season, while wildebeest and buffalo are important throughout the year.

Table 5.4. The influence of wildebeest and buffalo abundance on adult female lion group dynamics is important throughout the year while the influence of habitat variation is seasonal. The log-linear results show three separate one-way and one two-way interaction that influence adult female lions in the wet and dry seasons. In both seasons, the independent variables used included wildebeest (1)(W), coefficient of variation (V), habitat (H) and buffalo (2)(B_2) while the dependent variable was adult female group size (F). I have only presented significant interactions.

Effect	Model	L^2 [a]	ΔL^2 [b]	d.f.[c]	P[d]	Q^2 (%)[e]
Dry season						
No effects	[ ]	412.63		215		
No independent effects	[WVHB_2] [F]	82.64		107		
Baseline[f]	[WVHB_2] [FW] [FV] [FH] [FB_2]	75.05		98		
Wildebeest * Buffalo[g]	[WVHB_2] [FV] [FH] [FWB_2]		10.87	4	0.028	14.5
Wet season						
No effects	[ ]	688.81		215		
No independent effects	[WVHB_2] [F]	102.67		107		
Coefficient of variation[h]	[WVHB_2] [FV]		13.43	2	0.001	13.1
Buffalo[i]	[WVHB_2] [FB_2]		6.66	2	0.036	6.5
Baseline[f]	[WVHB_2] [FW] [FV] [FH] [FB_2]	81.26		98		
Wildebeest * Buffalo[g]	[WVHB_2] [FV] [FH] [FWB_2]		14.40	4	0.006	17.7

[a] L^2 = log-likelihood ratio
[b] ΔL^2 is the change in the log-likelihood ratio
[c] d.f.: where L^2 has been presented d.f. is the degrees of freedom for the model, where ΔL^2 has been presented d.f. is the change in degrees of freedom caused by the effect(s).
[d] P = the significance of the variable's effect.
[e] Q^2 is an R^2 analog that describes the amount of variation explained by the interaction terms that is not explained by the baseline model.
[f] The model incorporating all single order independent term effects.
[g] Model that describes the interaction of wildebeest and buffalo effects on exclusively adult female groups.
[h] The effect of coefficient of variation on exclusively adult female groups.
[i] The effect of buffalo abundance on exclusively adult female groups.
Note: B_2 is the buffalo abundance based on three abundance categories (Table 5.1).

Cubs

In the wet season, there were no interactions between the variables tested and cub groups on any level. Other factors such as adult male and female distribution might be more influential than habitat and prey during the wet season. In the dry season, wildebeest abundance alone influenced cub groups (Table 5.5). At both low and high levels of wildebeest abundance, there were more groups of three to four cubs than groups of either one to two or five to 16 cubs (Fig. 5.4). There were more large cub groups (five to 16) in areas of lower than higher wildebeest abundance (Fig. 5.4). For both groups of one to two and three to four cubs, there were more observations in the high than in the low wildebeest abundance areas (Fig. 5.4). While wildebeest abundance may be important to average cub groups, other factors such as adult female group size may be influencing larger cub groups.

Table 5.5. During the wet season, none of the variables tested influenced cub group dynamics, while during the dry season wildebeest abundance had a significant effect. I have only presented the significant log-linear results for cubs in the dry season. In both seasons the model used tested the influence of habitat (H), coefficient of variation (V), wildebeest (2)(W_2), and impala (2)(I_2) on cub group size (C).

Effect	Model	L^2 [a]	ΔL^2 [b]	d.f.[c]	P[d]	Q^2 (%)[e]
Dry season						
No effects	[ ]	377.02		215		
No independent effects	[HVW_2I_2] [C]	111.97		142		
Wildebeest[f]	[HVW_2I_2] [CW_2]		6.92	2	0.031	6.2

[a] L^2 = log-likelihood ratio

[b] ΔL^2 is the change in the log-likelihood ratio

[c] d.f.: where L^2 has been presented d.f. is the degrees of freedom for the model, where ΔL^2 has been presented d.f. is the change in degrees of freedom caused by the effect(s).

[d] P = the significance of the variable's effect.

[e] Q^2 is an R analog that describes the amount of variation explained by the interaction terms that is not explained by the baseline model.

[f] The effect of wildebeest abundance on cub groups.

Note: W_2 and I_2 are wildebeest and impala abundance based on two and three categories, respectively (Table 5.1).

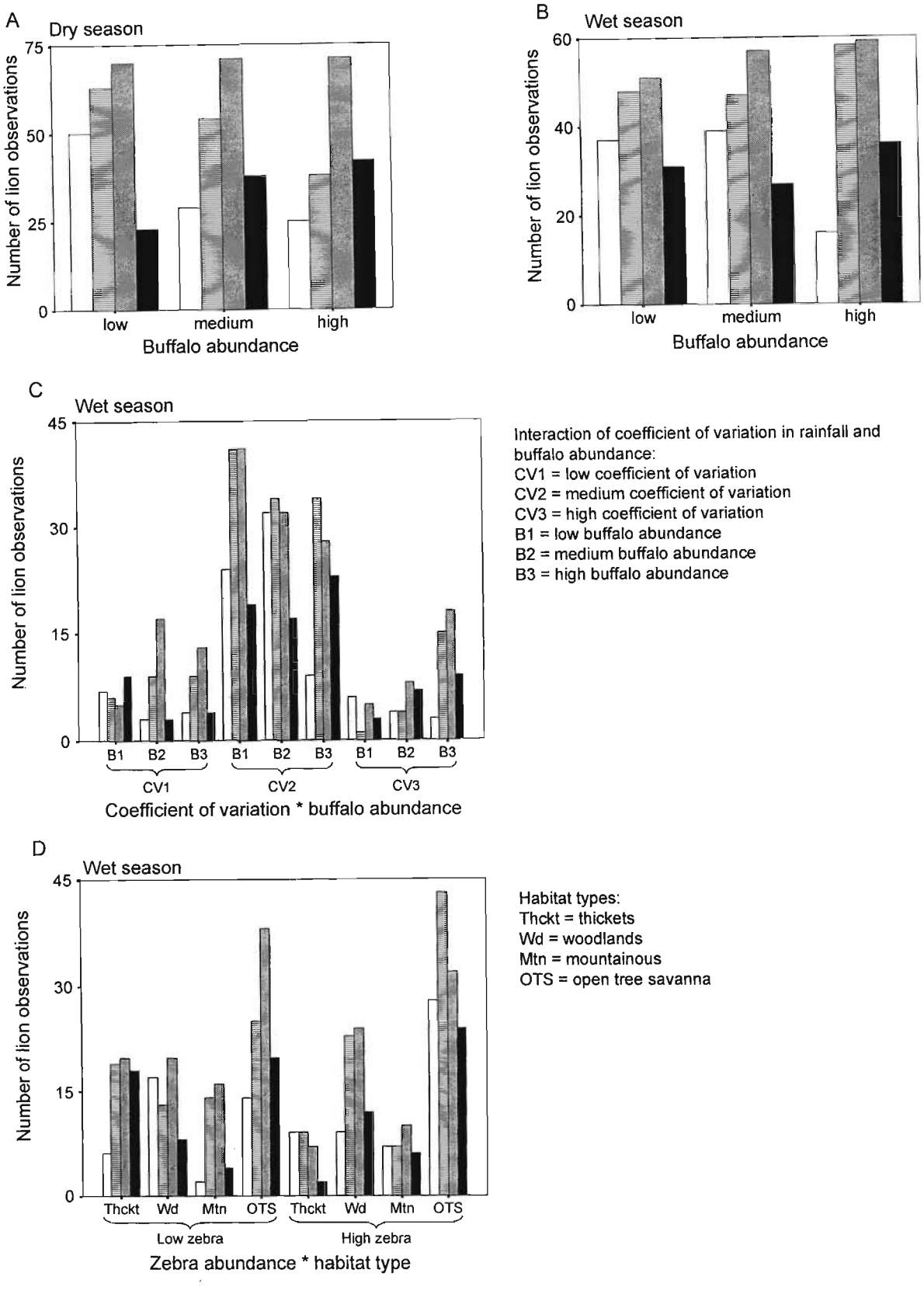

Figure 5.1. Adult lion group dynamics were influenced by different factors on a seasonal basis. However, in both seasons buffalo abundance (A & B) had an effect on total adult group size. During the wet season, there were also significant two-way interactions between adult group size and the coefficient of variation and buffalo abundance (C) and secondly, between adult group size and the habitat structure and zebra abundance (D). The open bars represent solitary individuals, striped bars represent groups of two, hatched bars represent groups of three to four and solid bars represent groups of five to 30. See the text for an explanation of these results.

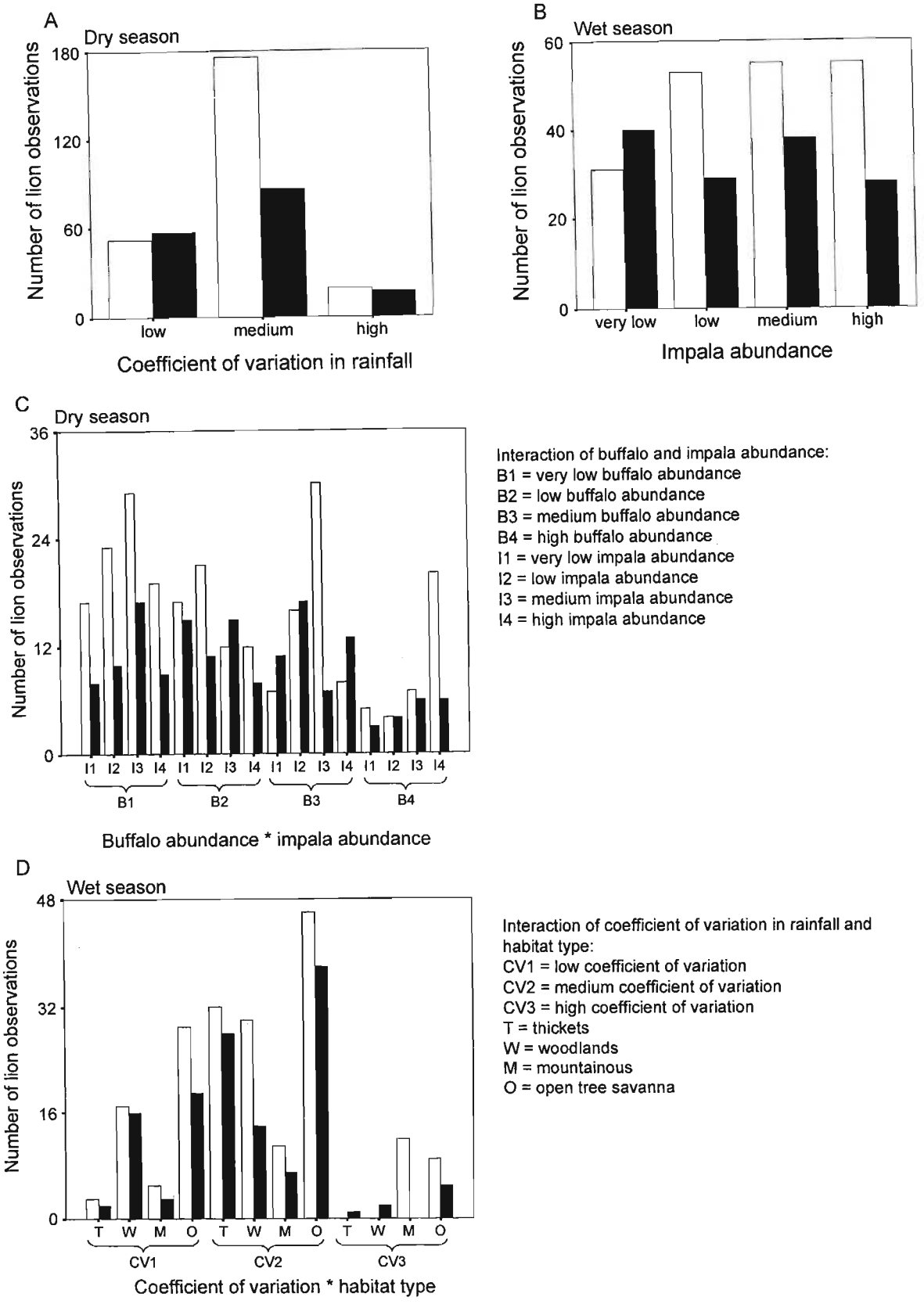

Figure 5.2. The effect of prey, habitat structure and rainfall variability on exclusively adult male group size differ on a seasonal basis. During the dry season, adult male group size was influenced by buffalo abundance (A) and the interaction between buffalo and impala abundance (C). While during the wet season, adult male group size was influenced by buffalo abundance (B) and the interaction between habitat structure and coefficient of variation in rainfall (D). The open bars represent solitary adult males while the shaded bars represent groups of males. See the text for an explanation of the results.

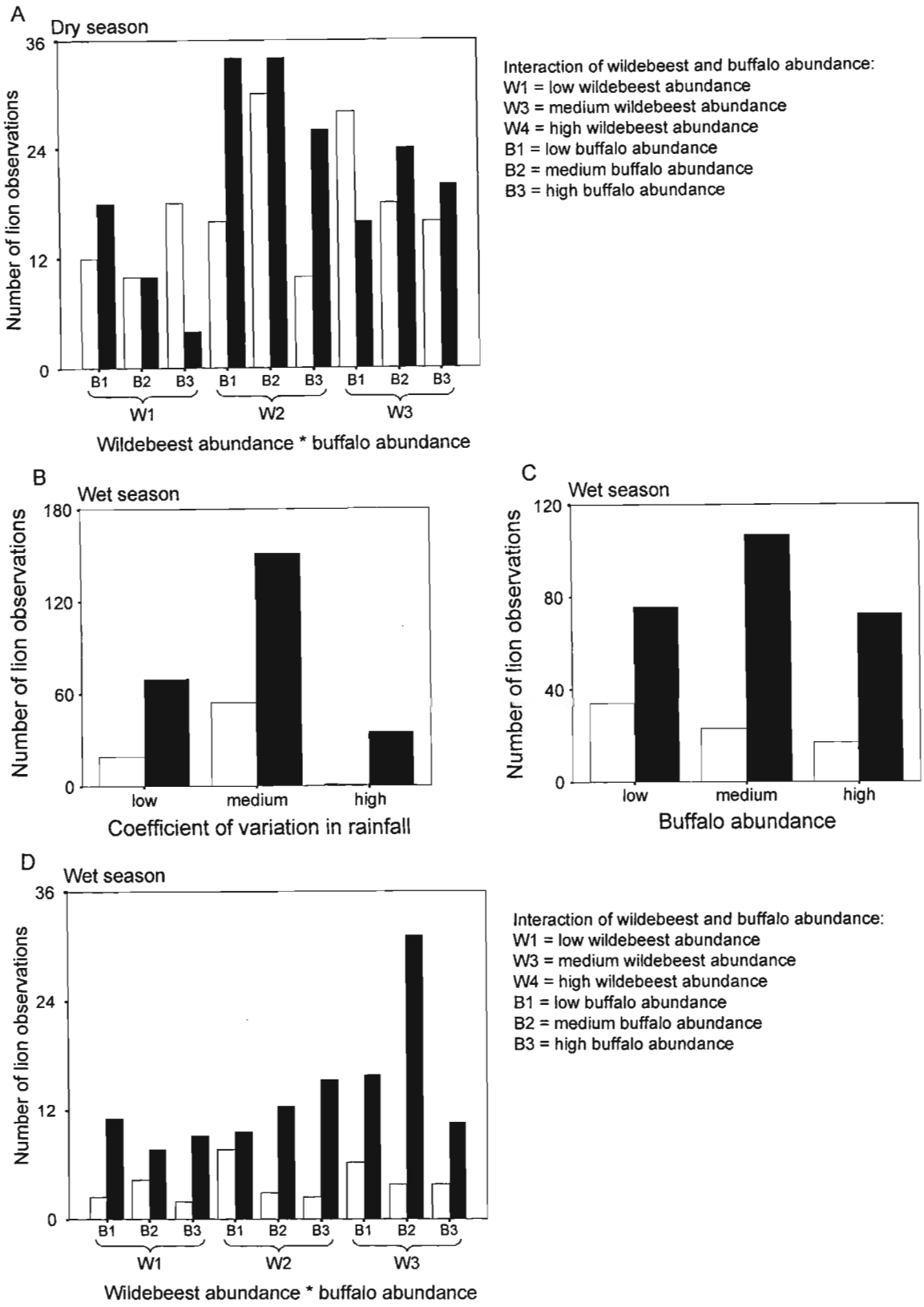

Figure 5.3. Adult female group size was affected by the prey abundance in both the wet and dry seasons. In the dry season, the interaction of wildebeest and buffalo abundance (A) affected group size. In the wet season, buffalo abundance alone (B), the coefficient of variation in rainfall (C) as well as the interaction of wildebeest and buffalo abundance (D) affected adult female group sizes. The open bars represent solitary adult females while the shaded bars represent groups of females. See the text for an explanation of the results.

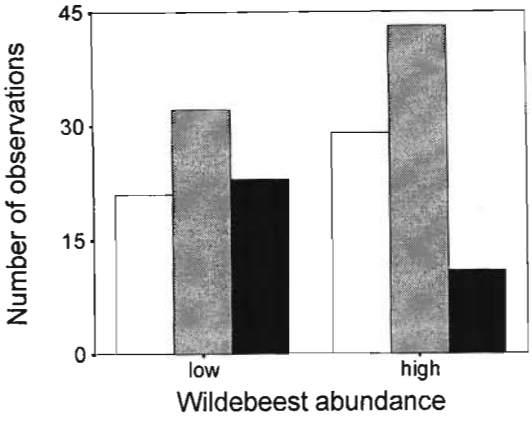

Figure 5.4. Cub group size was affected by wildebeest abundance in the dry season only. There were more groups of one to two cubs (open bars) and groups of three to four cubs (hatched bars) at high wildebeest abundance. While the number of observations of groups of five to 16 cubs (shaded bars) were greater at low wildebeest abundance.

Spatial patterns

Total adult group size

The general pattern of total adult group size distribution across KNP was similar for the dry and wet seasons (Figs 5.5 & 5.6, respectively). The areas where larger groups occurred were in close proximity across seasons (Figs 5.5 & 5.6). However, the distribution of these groups is influenced by different factors across seasons (see above section). I compared total adult group sizes in the dry season and the wet season with buffalo abundance, as the log-linear analysis highlighted this as an important factor affecting group size. In both seasons smaller adult groups (one to two individuals) were predominant in the areas of low buffalo abundance (Figs 5.5 & 5.6). Larger groups were present in the areas of medium to high buffalo abundance (Figs 5.5 & 5.6). Buffalo are an important prey species of lions, but they are not hunted by small groups of lions. Therefore, it is beneficial for the lions to form larger groups in order to hunt buffalo where they are in high abundance.

During the wet season, two two-way interaction effects also affected total adult group size; namely that of coefficient of variation in rainfall with buffalo abundance and habitat structure with zebra abundance. As the coefficient of variation falls within the medium category for a large area of the KNP, it was mainly the effect of buffalo abundance that affected group size in these areas (Fig. 5.7). However, where the areas of high variation in rainfall coincided with high buffalo abundance, there were mainly groups of three to four present (Fig. 5.7). In terms of the interaction effect of habitat structure and zebra abundance, there were larger groups of adults in the mountainous areas of south-western KNP where zebra abundance was high (Fig. 5.7). In the

central area of KNP where zebra abundance is high in the open tree savanna habitat there were generally groups of three and more adults (Fig. 5.7).

Exclusively adult male groups

In the dry season, the coefficient of variation and the two-way interaction between buffalo and impala abundance were found to influence adult male group dynamics. In terms of spatial patterns of distribution, males were predominantly solitary in the areas of high rainfall variation along the south-eastern border of KNP (Fig. 5.8). As the area of medium rainfall variation covers most of KNP, the distribution of solitary males and groups of males in this region was approximately equal (Fig. 5.8). The interaction effect of buffalo and impala abundance on adult male group size was such that solitary individuals were mainly associated with areas of very low buffalo abundance regardless of impala abundance (Fig. 5.9). Groups of adult males occurred in the areas of high buffalo and high impala abundance as well as those areas where buffalo abundance was very low but impala abundance was high (Fig. 5.9).

In the wet season, exclusively adult male groups occurred mainly in the areas of high impala abundance in central KNP and along the eastern side of KNP between the central and southern areas (Fig. 5.10). There were very few areas where large groups occurred at very low impala abundance (Fig. 5.10). The interaction of habitat structure and the coefficient of variation in rainfall also affected adult male group sizes in the wet season. Groups of adult males occurred in the northern thickets where the variation in rainfall ranged between 26 and 29% (medium variation, Fig. 5.11). Groups of adult males were also associated with the open tree savanna regardless of the variation in rainfall (Fig. 5.11).

Exclusively adult female groups

In northern KNP during the dry season, there were predominantly groups of adult females in the area of low buffalo abundance where wildebeest abundance ranged between low and high (Fig. 5.12). Although buffalo and wildebeest were both in high abundance in the extreme northern section there were mainly solitary females in this area (Fig. 5.12). In central KNP, the groups of females occurred in the areas of low buffalo but high wildebeest abundance (Fig. 5.12). While in the south-western section, adult female groups occurred in the areas of low to high wildebeest abundance where buffalo abundance also ranged between medium and high (Fig. 5.12).

During the wet season, the coefficient of variation in rainfall affected adult female group dynamics. However, in terms of the spatial distribution of adult female group sizes across these

regions, the main difference occurred in the area of medium variability, where there were more solitary females in the northern half of KNP than the southern (Fig. 5.13).

Buffalo abundance also affected adult female group size in the wet season. While groups of females were predominant throughout the park, solitary individuals occurred mainly in the areas of low to medium buffalo abundance in the central and northern areas of KNP (Fig. 5.14). The interaction of the buffalo and wildebeest abundance also had an effect on female group size during the dry season. However, this pattern was not clear on a spatial scale due to the presence of groups of females throughout the park (Fig. 5.15). When females were solitary, it was predominantly in the areas of low buffalo and medium wildebeest abundance in central KNP and low to medium buffalo abundance with low wildebeest abundance in the north (Fig. 5.15).

Cubs

Cub group size in the wet season was not affected by any of the variables studied. However, during the dry season, wildebeest abundance had an effect. Although groups of three to four cubs were predominant throughout the park, the area was interspersed with very small groups in the central and southern regions (Fig. 5.16). Larger groups occurred in a large area along the north-western border and in small areas throughout KNP (Fig. 5.16). The areas of large cub group sizes generally coincided with the areas of low wildebeest abundance (Fig. 5.16). The small cub group sizes (one to two) occurred in the areas of high wildebeest abundance in the south, but in the areas of low wildebeest abundance in central KNP (Fig. 5.16).

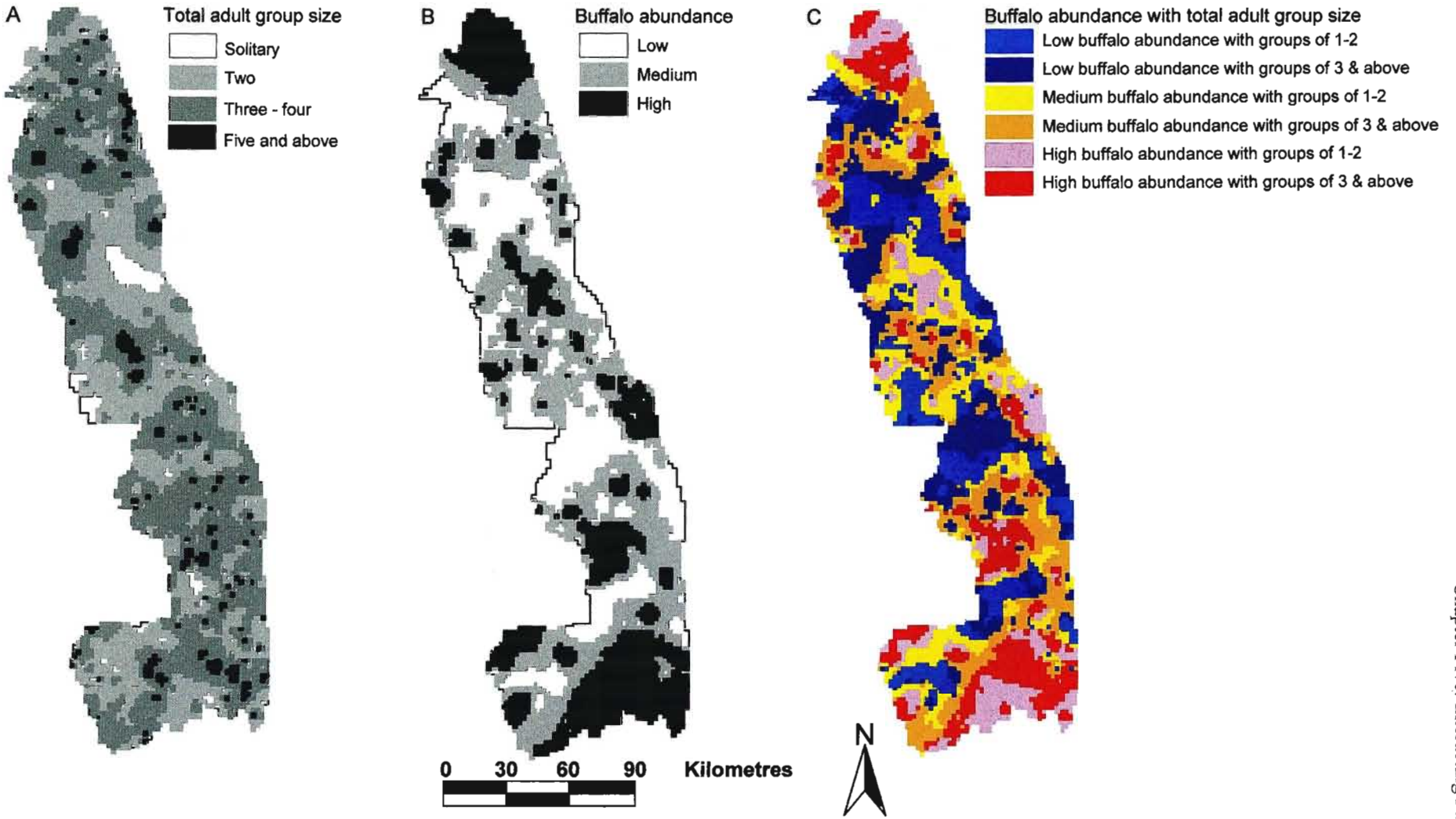

Figure 5.5. The surface map showing the distribution of maximum total adult group sizes (A) was overlaid on the buffalo abundance map (B) to determine the spatial distribution of total adult groups through KNP during the dry season (C). For ease of interpretation only two measures of group size (one to two and, three and above) were used for the map combining buffalo abundance and group size (C). Smaller groups were present predominantly in areas of low buffalo abundance while larger groups were present in areas of medium to high buffalo abundance (C). The categories of buffalo abundance are listed in Table 5.1. Grid cell size = one minute².

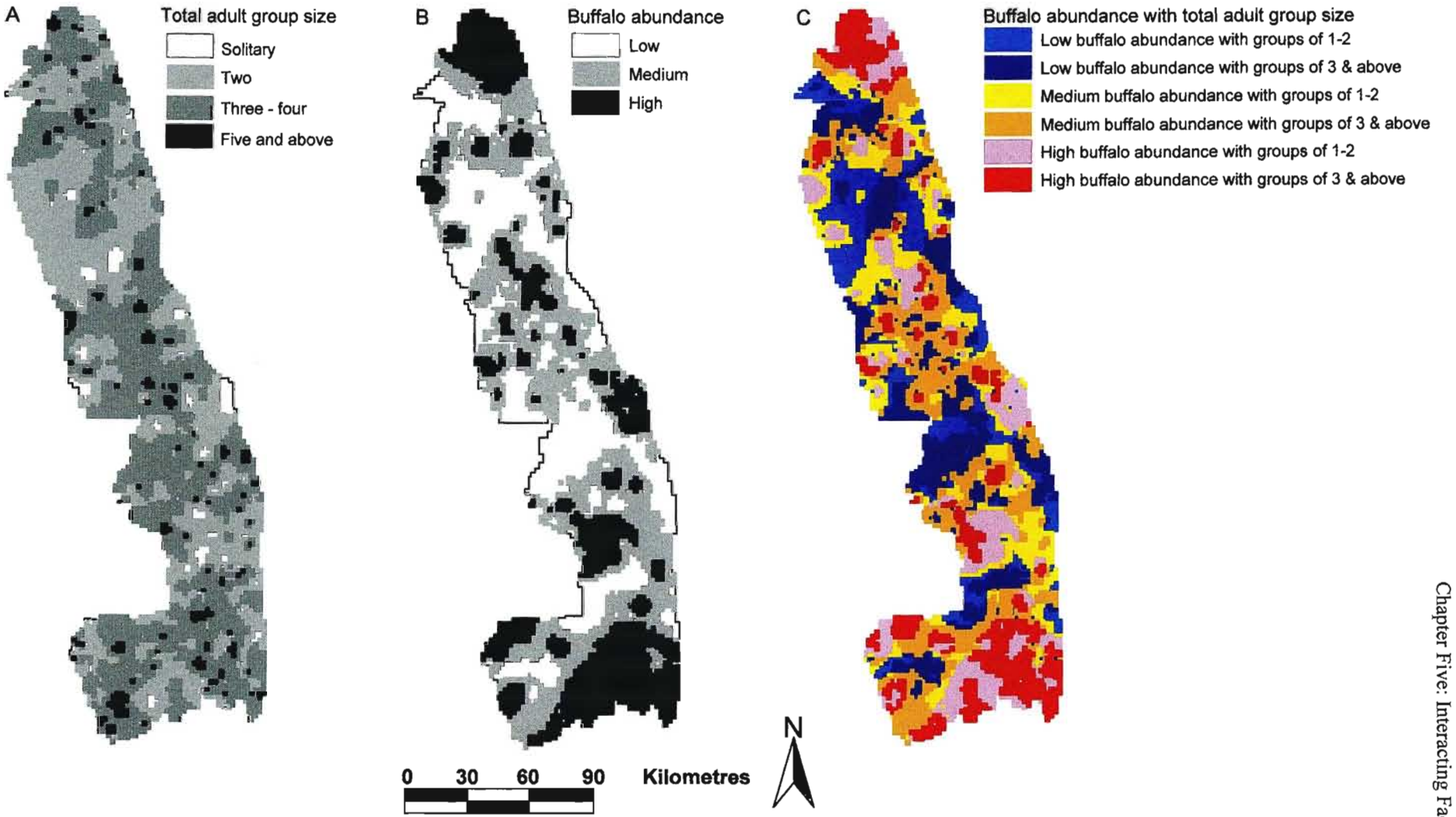

Figure 5.6. The surface map showing the distribution of maximum total adult group sizes (A) was overlaid on the buffalo abundance map (B) to determine the spatial distribution of total adult groups through KNP during the wet season (C). For ease of interpretation only two measures of group size (one to two and, three and above) were used for the map combining buffalo abundance and group size (C). Larger groups were present in areas of medium to high buffalo abundance while smaller groups were predominant in area of low buffalo abundance (C). The categories of buffalo abundance are listed in Table 5.1. Grid cell size = one minute².

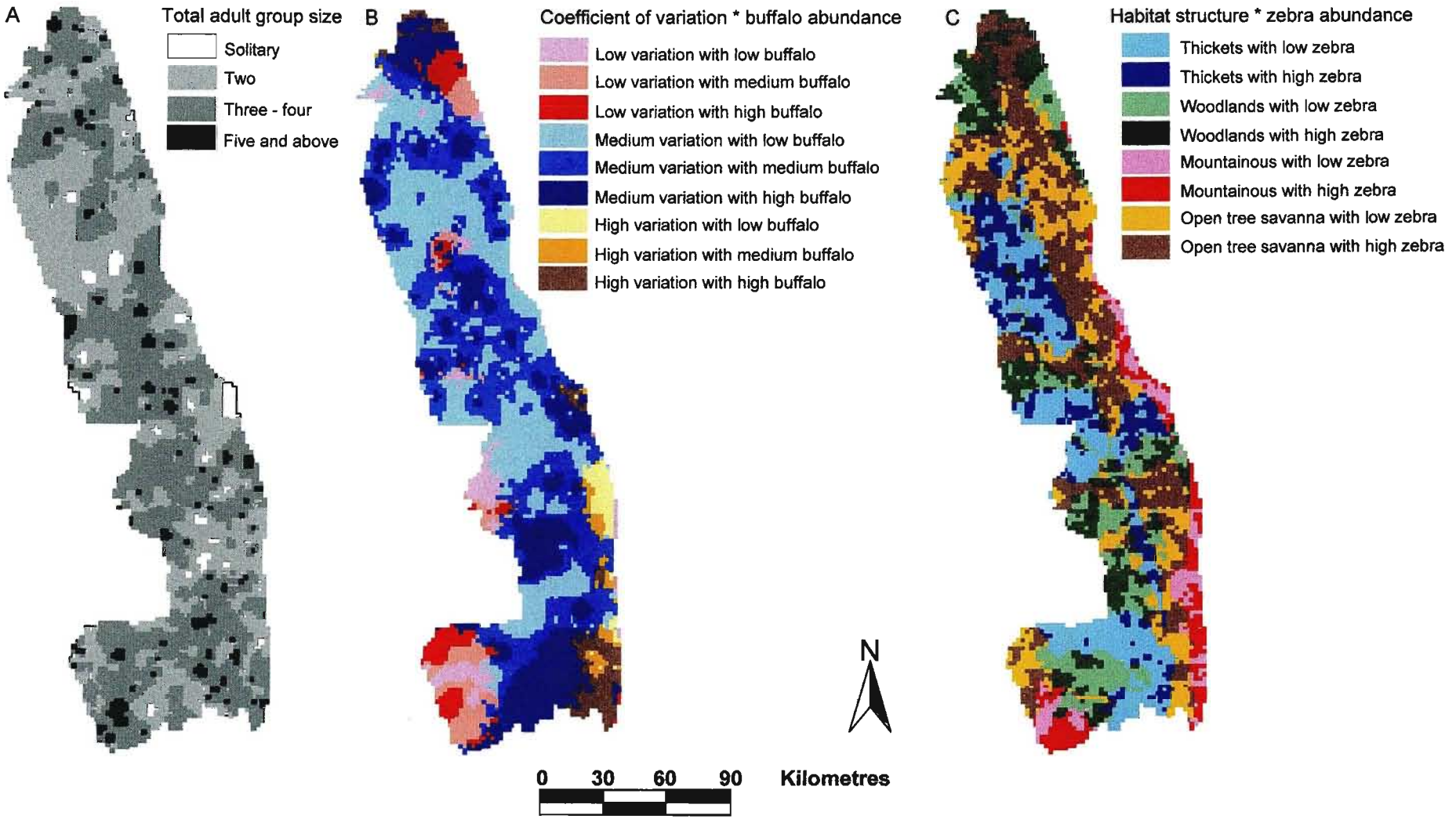

Figure 5.7. In the wet season, larger groups of adults (A) predominated in the areas of medium habitat variation (26-29%) regardless of buffalo abundance (B). However, this variation category covers most of KNP. Larger groups of adults (A) were associated with areas of increasing buffalo abundance in the areas of high variation (B). More solitary adults and groups of adults (A) were found in the open tree savanna and woodland habitats, regardless of the zebra abundance (C). The categories of the coefficient of variation in rainfall, buffalo and zebra abundance are defined in Table 5.1. Grid cell size = one minute².

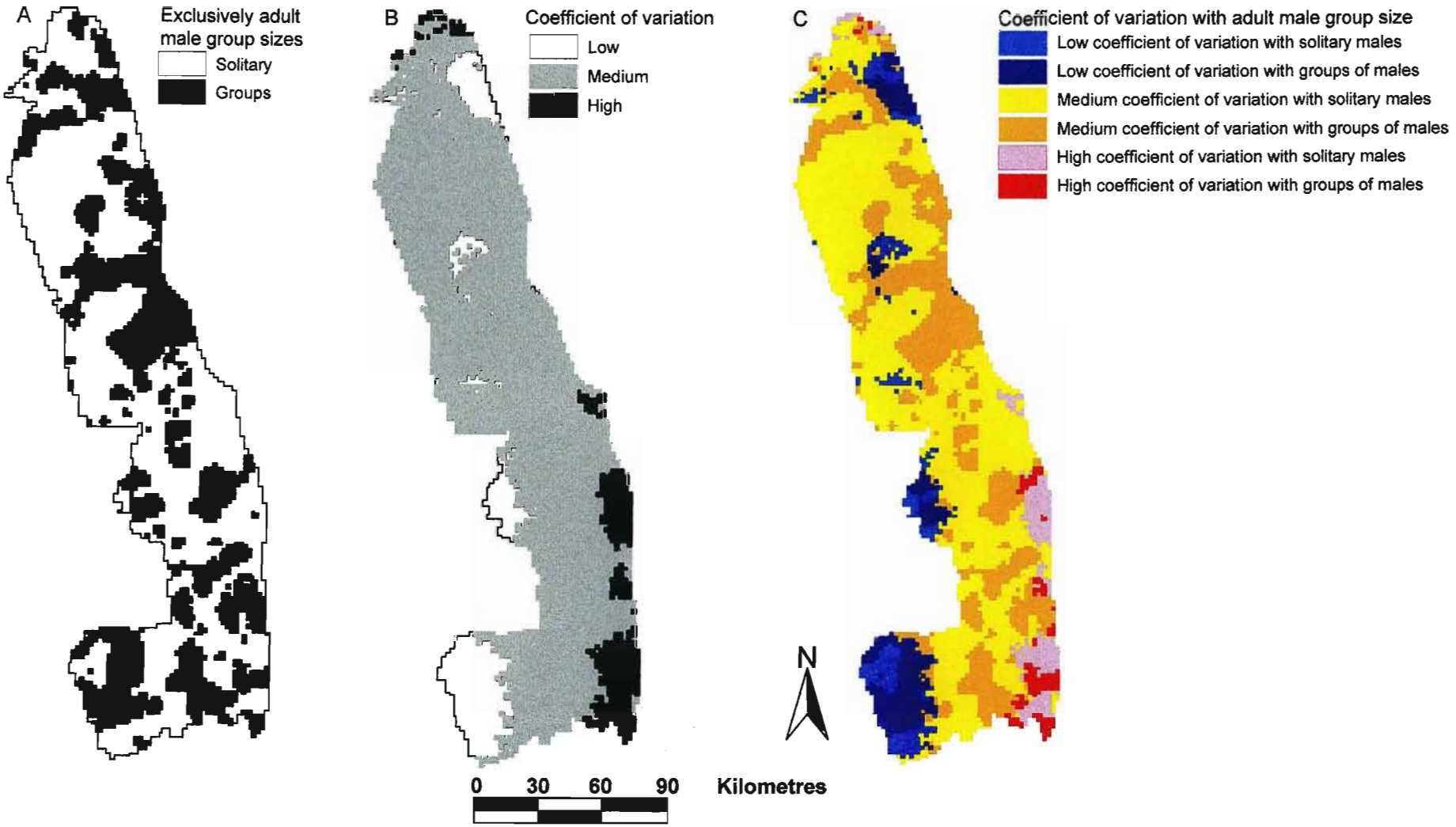

Figure 5.8. The surface map showing the distribution of maximum exclusively adult male group sizes (A) was overlaid on the coefficient of variation in rainfall map (B) to determine the spatial distribution of adult male groups through KNP during the dry season (C). The categories of the coefficient of variation in rainfall are defined in Table 5.1. Grid cell size = one minute².

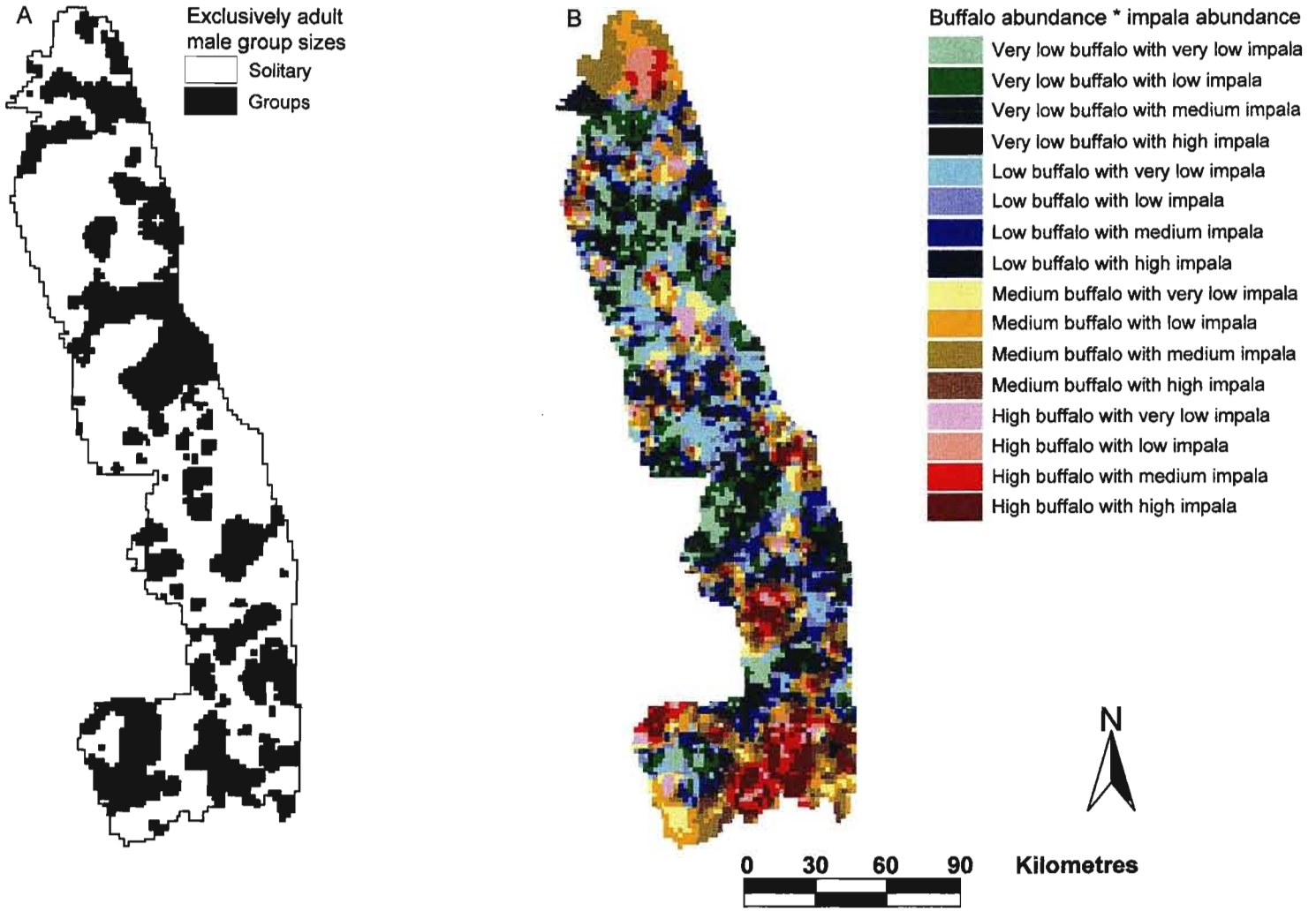

Figure 5.9. The surface map of maximum exclusively adult male group sizes in the dry season (A) was compared to the map showing the interaction of buffalo and impala abundance (B). Solitary males predominated in the areas of low buffalo abundance regardless of impala abundance. Groups of adult males occurred in the areas of high buffalo abundance at all levels of impala abundance and in the areas of low buffalo abundance where impala abundance was high. The categories of buffalo and impala abundance are defined in Table 5.1. Grid cell size = one minute².

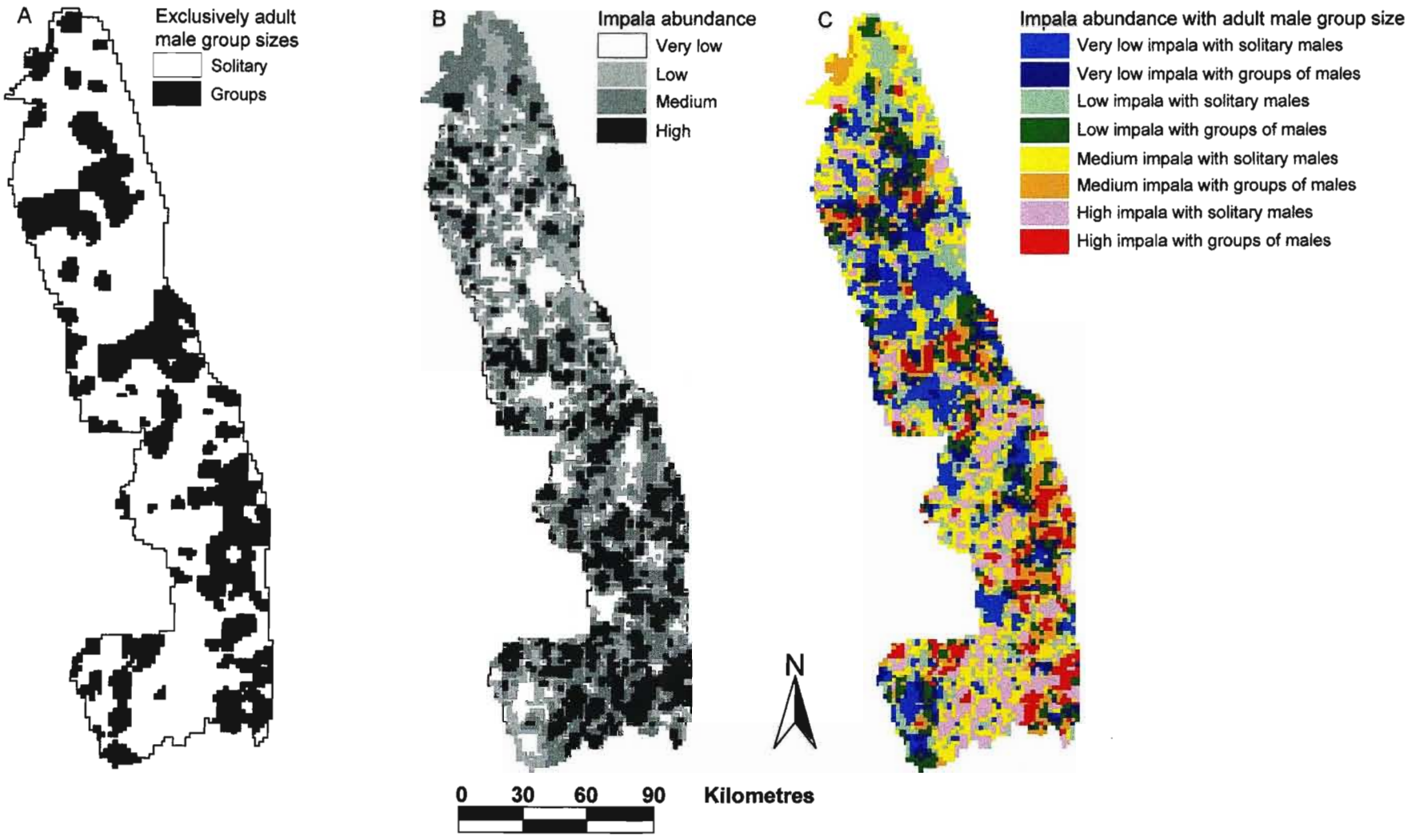

Figure 5.10. The surface map showing the distribution of maximum exclusively adult male group sizes (A) was overlaid on the impala abundance map (B) to determine the spatial distribution of adult male groups through KNP during the wet season (C). Adult males were generally solitary during the wet season (A). Although adult males occurred in groups in all areas of impala abundance, they were predominantly in groups in areas of high impala abundance (C). The categories of the impala abundance are defined in Table 5.1. Grid cell size = one minute².

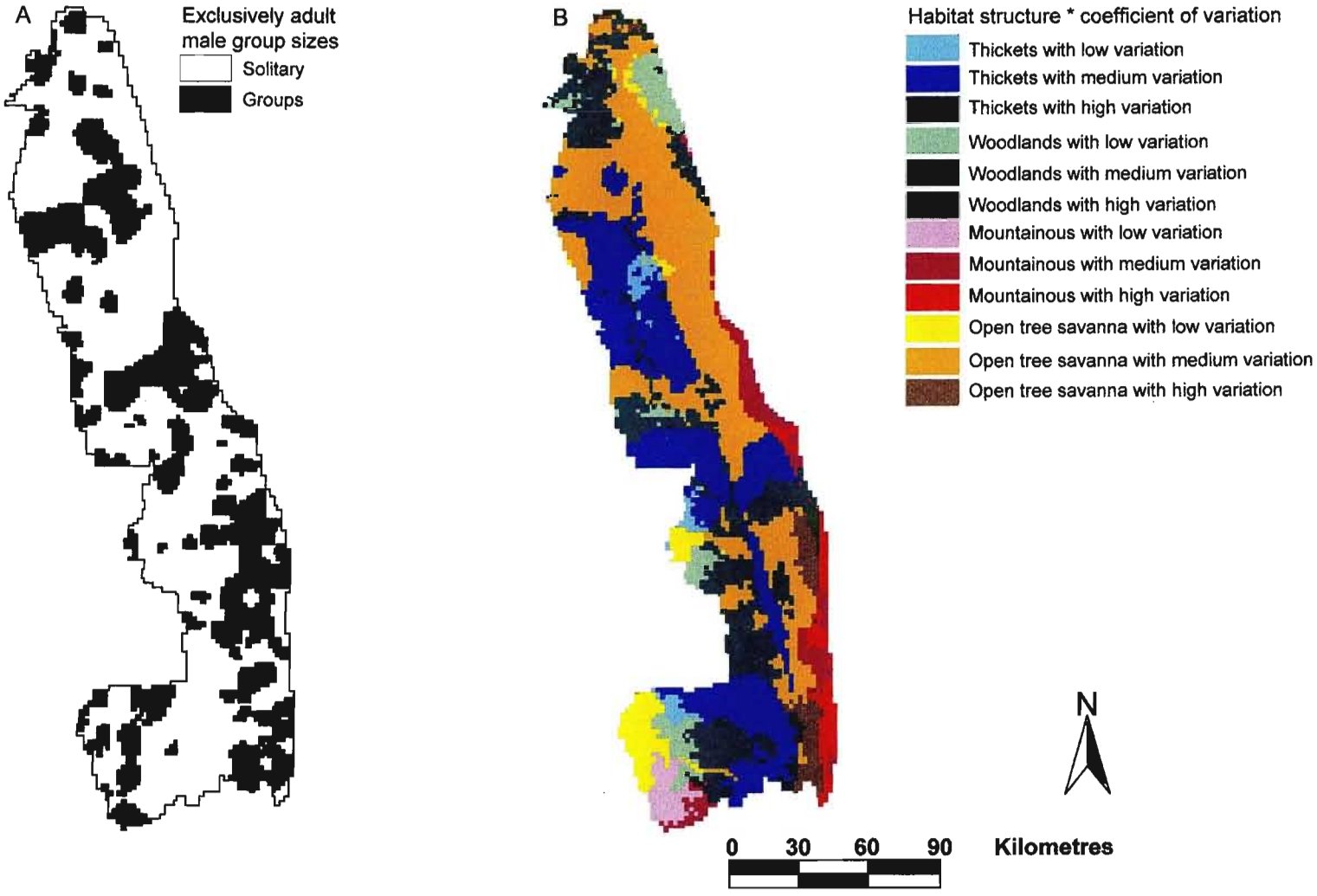

Figure 5.11. In the wet season, maximum exclusively adult male group size (A) was affected by the interaction of habitat structure and the coefficient of variation in rainfall (B). There were greater numbers of solitary and groups of males in the areas of medium variation within the thickets and open tree savanna (C). The categories of the coefficient of variation in rainfall are defined in Table 5.1. Grid cell size = one minute^2.

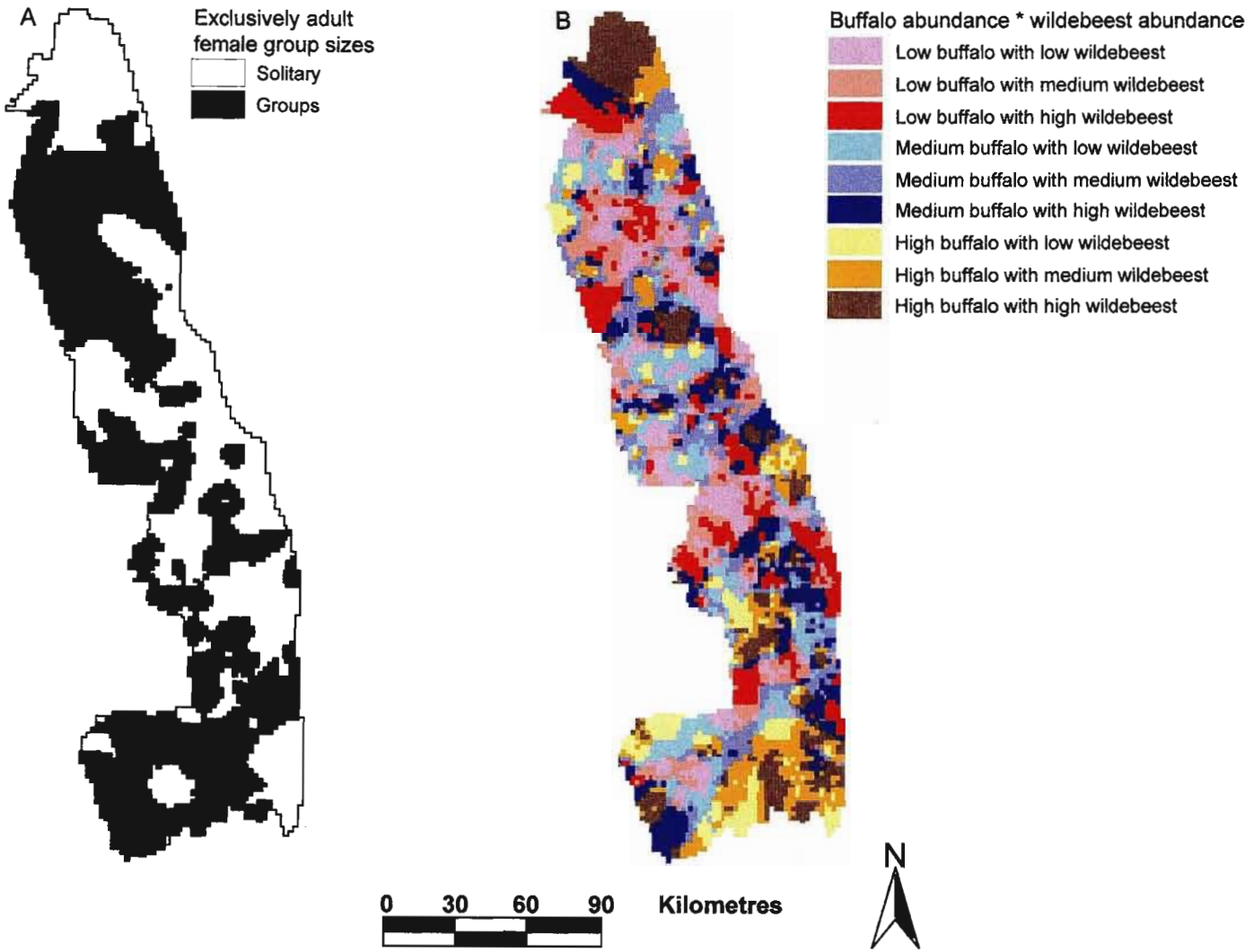

Figure 5.12. The surface map of maximum exclusively adult female group size in the dry season (A) was contrasted with the interaction map of buffalo and wildebeest abundance (B). Groups of females occurred in areas where wildebeest were abundant regardless of buffalo abundance. While solitary females occurred in areas of medium to high wildebeest abundance where buffalo abundance was low to medium. The categories of buffalo and wildebeest abundance are defined in Table 5.1. Grid cell size = one minute^2.

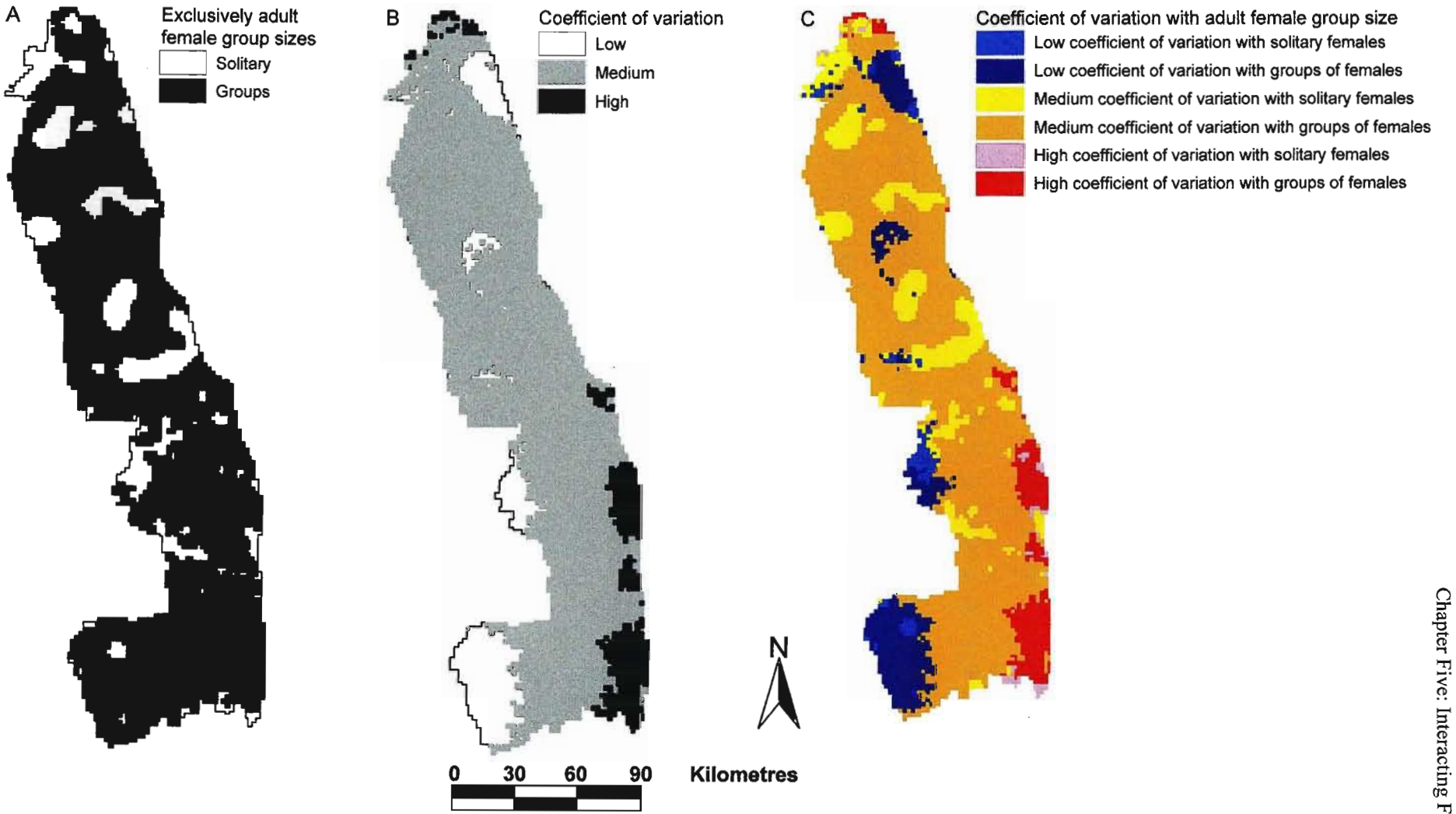

Figure 5.13. The surface map showing the distribution of maximum exclusively adult female group sizes (A) was overlaid on the coefficient of variation in rainfall map (B) to determine the spatial distribution of adult female groups through KNP during the wet season (C). As adult females were generally in groups during the wet season there was little difference in the distribution of group sizes across coefficient of variation regions. However, where females were solitary, it was mainly in regions of low to medium variability (C). The categories of the coefficient of variation in rainfall are defined in Table 5.1. Grid cell size = one minute^2.

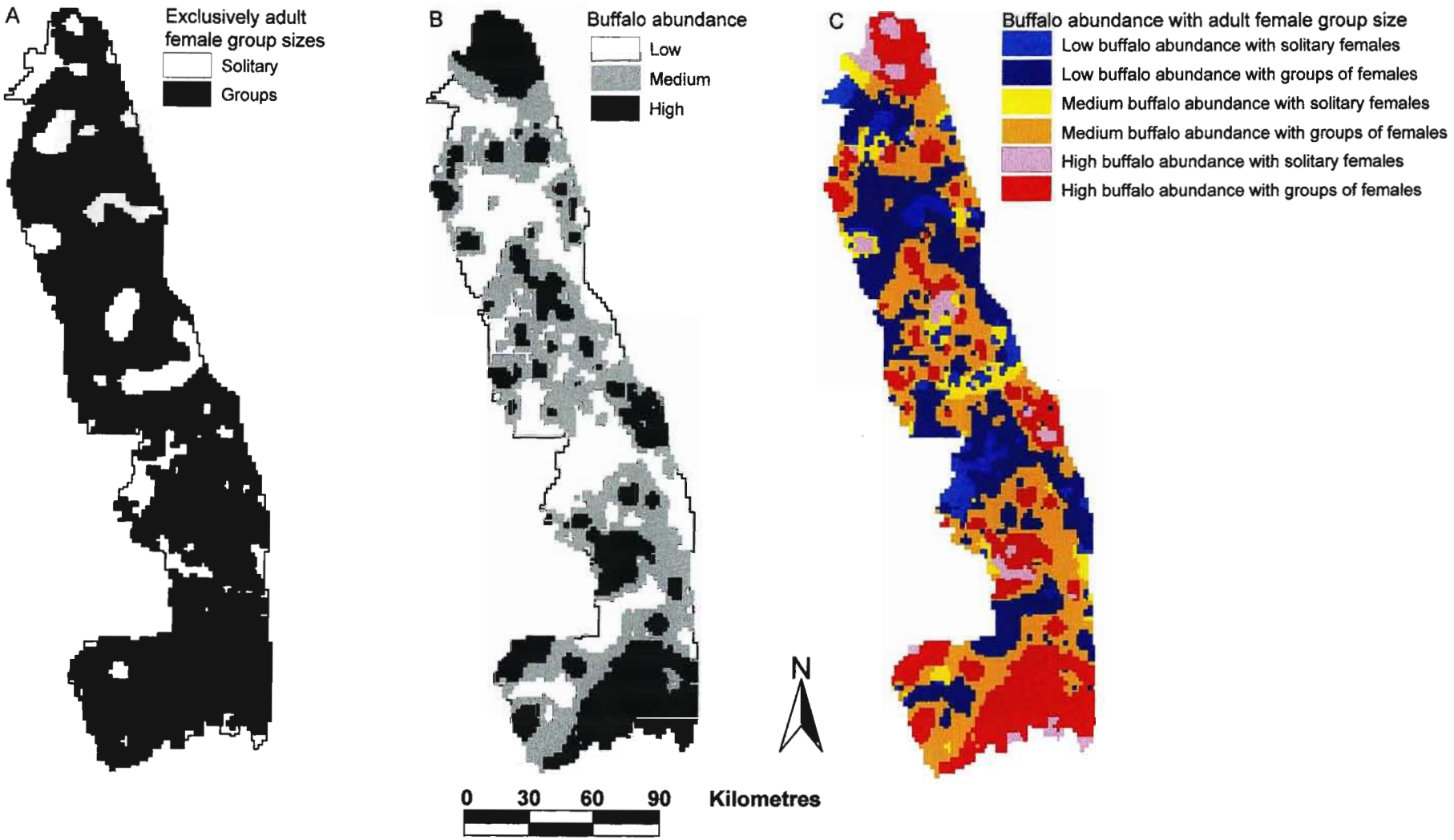

Figure 5.14. The surface map of maximum exclusively adult female group size (A) was overlaid on the map of buffalo abundance (B) to determine adult female group size distribution across KNP during the wet season (C). Groups of females were predominant throughout the park. However, solitary females were mainly present in the areas of low to medium buffalo abundance (C). The categories of buffalo abundance are listed in Table 5.1. Grid cell size = one minute².

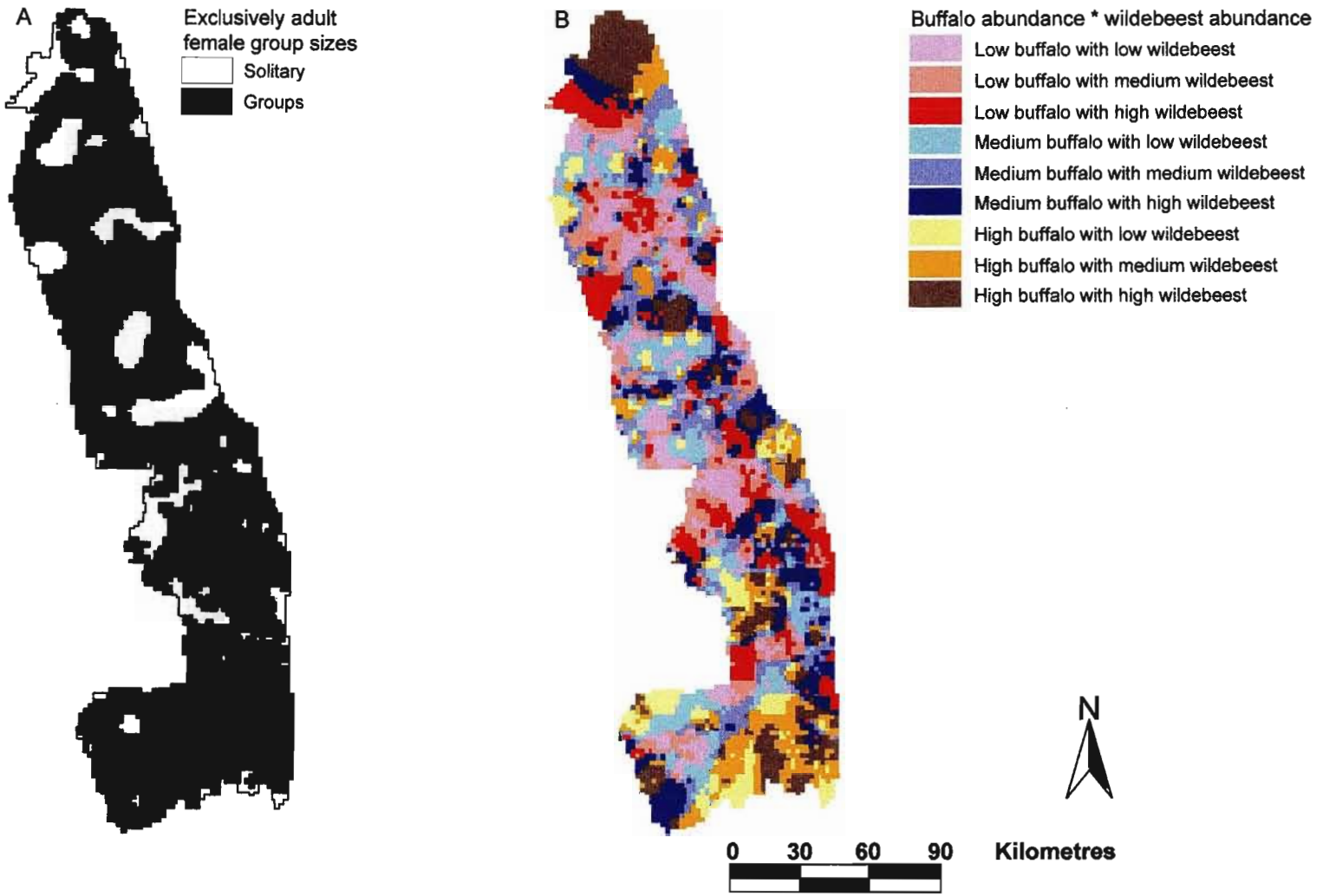

Figure 5.15. The surface map of maximum exclusively adult female group size in the wet season (A) was contrasted with the interaction map of buffalo and wildebeest abundance (B). Adult females were predominantly in groups throughout KNP during the wet season. Areas with solitary females fell in low to medium buffalo abundance regions where wildebeest abundance ranged from low to high. The categories of buffalo and wildebeest abundance are defined in Table 5.1. Grid cell size = one minute².

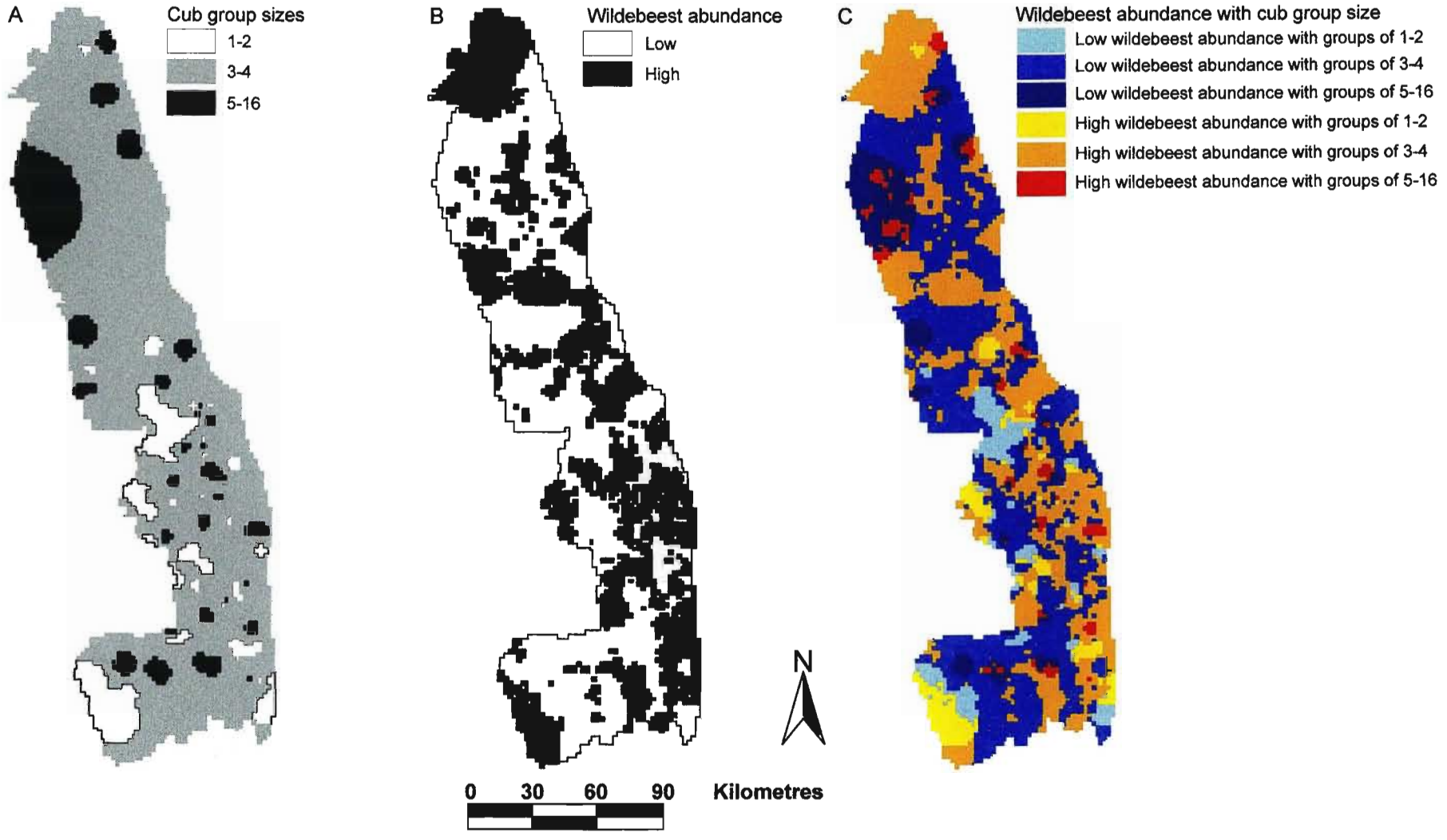

Figure 5.16. The surface map of maximum cub group sizes in the dry season (A) was overlaid on the map of wildebeest abundance (B) to determine the distribution of cub groups in the abundance regions across KNP during the dry season (C). Cub group sizes of three to four were predominant throughout KNP (A). Larger cub groups occurred in areas of low wildebeest abundance in the south and north (C). Groups of one to two cubs occurred in southern KNP at high wildebeest abundance and in central KNP where wildebeest abundance was low (C). The categories of wildebeest abundance are listed in Table 5.1. Grid cell size = one minute^2.

Discussion

There are many factors that influence group dynamics and animal distribution. However, due to limitations of data collection, these factors are often studied separately without taking other biological and behavioural factors into account (Sinclair 1985; McComb, Packer & Pusey 1994; Farnsworth & Beecham 1999). However, when studying multiple factors, it is important to be able to distinguish between the relative contribution of each factor to the ecological pattern studied (Franklin 1989). For this reason, the temporal scale of the project is important, as the wrong conclusions can be drawn from short-term results or results that focus on one season or period only (Franklin 1989). In this chapter, I have brought together measures of habitat quality and resource availability to determine which influence lion group dynamics and how. I have used seven to eight years of data in order to increase my confidence in the results obtained. By working with the data from KNP, it has also given a broader spatial scale to the project that is often limited in other studies (see Chapter One). By working on a large spatial scale changes in environmental determinants and the combinations thereof can be separated and their effects more clearly determined.

In this study, as found in previous studies, wildebeest were important to adult female group dynamics while impala and buffalo were important to adult males (Rudnai 1974; Scheel 1993; Funston *et al.* 1998). Buffalo abundance was important to the total adult group size/ functional group size in both seasons. The effect of habitat quality as defined by the coefficient of variation in rainfall, was important to the functional group size and groups of exclusively adult males or females. However, in terms of the functional group, rainfall variability was only important in the wet season and in combination with buffalo abundance, with larger groups occurring in the areas of medium variability regardless of buffalo abundance. In the dry season, there were more groups of females than solitary females in more variable environments. This is in agreement with the studies of Packer *et al.* (1990) and Stander (1992b) that found it was more beneficial for females to form larger groups when prey were scarce in order to attain their daily minimum food requirements. Larger groups are able to hunt larger prey and hunting success rate increases with an increase in hunting group size (Schaller 1972; Packer & Ruttan 1988), which may be important factors in more variable habitats. Males occurred on their own more often in variable environments. Packer *et al.* (1990) found that solitary females could attain their minimum daily requirements when prey were scarce as they did not have to share their meal. The same principle may apply to solitary males in variable environments. There may also be other behavioural and social aspects that result in solitary males occurring more frequently in variable

environments. Non-territorial males, especially solitary males, may avoid areas held by territorial coalitions by spending time in less favourable habitats.

Cubs were influenced by wildebeest abundance only during the dry season. Cub survival and group size however may be influenced to a greater degree by behavioural and social factors. Cub litter size may be influenced by that of other females in the group, which would then affect the total cub group size (Packer & Pusey 1995). Adult males also influence cub survival, as new males taking over a pride will kill the young cubs present (Pusey & Packer 1994).

Although mechanisms, based on single factors, that are used to explain group dynamics are useful for determining which of these factors is important to group dynamics, they often cannot explain all the variance in the data. The assumptions of these models or theories may also not fit perfectly with field experiments and studies where elements cannot be controlled as they can be in a laboratory experiment. For example, ideal free distribution (IFD) assumes that competitors are equal, and are free to settle in the optimal area for optimal fitness benefits (Fretwell & Lucas 1970). However, lions are territorial predators that are not equal competitors. Therefore some groups may settle in the resource-rich areas while others will have no choice but to settle in the resource-poor areas. A model such as the perception limitation model (PLM) may better explain lion distribution, as it allows for unequal intake rates and for the fact that the lions may not have complete knowledge of available patches and patch quality (Abrahams 1986). However, neither of these models takes into account the behavioural relationships of lions, both within their prides and between prides. As lions are territorial animals they will defend an area that changes very little through time (Bertram 1973). They are also highly mobile, covering up to 35km in a night (Eloff 1973). Therefore, while part of their territory may not be rich in prey, they are able to move great distances to find food, water or shelter for cubs. Another alternative is the mechanism explained by the marginal value theorem (MVT)(Charnov 1976) that allows for a decrease in food availability over time spent in an area. However, it does not allow for revisiting of sites. This is an unrealistic assumption in terms of my data as prey move on a temporal basis and may revisit the same sites on a daily/ weekly/ monthly/ seasonal basis therefore resulting in the predators (lions) revisiting the same patches.

The resource dispersion hypothesis (RDH) describes why groups should form and what should influence territory size. In terms of social predators, group size is often correlated with prey density (Creel & Macdonald 1995), smaller predator groups occurring where their prey is least abundant and, larger groups occurring where prey is in great abundance. However, there are

also other behavioural and biological factors that will affect the group size of social predators such as relatedness between individuals (Ross *et al.* 1996), territory defence (Pusey & Packer 1994) and defence of young (Pusey & Packer 1994). In terms of territory size, lions have territories that vary very little in size over time regardless of pride size (Bertram 1973). Therefore territory size of lions may be better described by a model of territory inheritance or of constant territory size in fluctuating environments (Meia & Weber 1996).

Risk-sensitive foraging is also limited as, like the above mechanisms, it only deals with the effect of variability in resource availability on foraging strategies (Stephens & Krebs 1986). Packer *et al.* (1990) determined that food alone could not fully account for different lioness group sizes. Social and behavioural factors may play a more important function (Packer *et al.* 1990). This may also be extended to other animals, where group formation and distribution is not only affected by resource variability but also by the presence of competitive species (Sinclair 1985; Carbone *et al.* 1997; Mills & Gorman 1997).

Therefore, while the above-mentioned hypotheses and models are useful for interpreting the importance of ecological determinants on an individual level, it is rather a combination of these ideas that should be used to explain the interaction and combination of environmental factors that is necessary to influence spatial socio-ecology.

The scale over which a study is performed is an important factor when determining the influential patterns and processes that affect spatial socio-ecology. Large differences in patterns or processes at a small scale may be less distinct when taken over a larger region (Levin 1992). The reverse is also true for processes and patterns that act on a large scale. When a study is conducted over a small area within which there is little variation in certain patterns, their importance in determining animal distribution may be underestimated. Working with the KNP data has allowed me to examine the effects of habitat, rainfall and resource patterns and processes on lion group dynamics over a large area and over an eight-year period. Although there were biases involved in working with an historical database, the data were useful for determining the broad scale influences. While certain factors were found to have important effects on group dynamics in the log-linear analyses, their influence on lion group dynamics varied on a spatial scale across KNP. This shows that although these factors might be driving group dynamics in certain areas, their effect may be less pronounced in others because of the interaction effects of numerous environmental elements.

Although lion group dynamics are influenced to a large extent by social interactions, there are environmental patterns and processes that influence the distribution of groups through space and time. Prey abundance, the variability in rainfall and the structure of the habitat all influence lion group dynamics. However, their importance varies through space and time as well as with the lion group type studied.

CHAPTER SIX
SUMMARY & CONCLUDING REMARKS

Numerous patterns and ecological processes influence environments, and the distribution of plants and animals within them. These patterns and processes vary through space and time (Addicott *et al.*1987; Menge & Olson 1990; Christensen 1997). Their effects can be studied on a number of different levels or scales, both spatial and temporal. Although it is often more feasible to study the effects of these factors separately; examination of the combination and interaction of factors may better explain the relative importance of each factor on a larger scale. Thus the scope of a project may influence the results obtained.

This study was conducted using the lion observation records from the Kruger National Park. The lion data covered a 29-year period and was collected through an area of 20 000km^2. It therefore had the advantage of a large spatial and temporal scale. By studying the influence of both biotic patterns and abiotic processes, it allowed me to discern between the importance of these factors through space and time. I initially studied the factors (habitat structure, prey and habitat variability) separately in order to determine if they influenced lion group dynamics at all and if so, how. I then looked at the combined influence of selected factors to determine if it was the interaction of these elements that was important or if one factor alone had a greater impact on group dynamics.

The main results of this project were as follows:

1. Lions select open tree savanna and thickets (Chapter Two).
2. Subadult and cub groups were largest in the woodlands (Chapter Two).
3. Male group size increased with an increase in buffalo and impala abundance. Groups were also larger where buffalo contribution to the total prey base available was high (Chapter Three).
4. Total group size increased with an increase in impala abundance (Chapter Three).
5. Total group size was largest at buffalo kills (Chapter Three).
6. Adult male group size was largest at buffalo and giraffe kills (Chapter Three).
7. Adult female group size was largest at buffalo and giraffe kills (Chapter Three).
8. Male presence at buffalo kills was higher than expected by chance (Chapter Three).
9. Total group size, adult male group size and adult female group size was positively correlated with the coefficient of variation in rainfall (Chapter Four).

10. Buffalo abundance had an effect on total adult group size in both the wet and dry seasons, with smaller groups in areas of low buffalo abundance (Chapter Five).
11. In the wet season, total adult group size was also affected by the interaction of the coefficient of variation in rainfall and buffalo abundance. Larger groups predominated in the areas of high variation in rainfall where buffalo abundance was high. (Chapter Five).
12. In the wet season, total adult group size was also affected by the interaction of habitat structure and zebra abundance. Most groups were observed in the open tree savanna regardless of zebra abundance (Chapter Five).
13. In the dry season adult males were affected by the coefficient of variation in rainfall, with more solitary males than groups of males in areas of high variation. The two-way interaction of impala and buffalo influenced adult male groups. Males on their own were predominant in areas of higher impala abundance and very low to medium buffalo abundance while groups of males were present to a larger degree in areas of both medium to high impala and buffalo abundance (Chapter Five).
14. In the wet season adult males were affected by the impala abundance as well as by the interaction of the coefficient of variation in rainfall and habitat structure. More single males than coalitions occurred in areas of low to high impala abundance. There were more solitary males and groups of males in areas of medium variation in two habitats, the thickets and open tree savanna (Chapter Five).
15. Adult female group size was affected by the interaction of wildebeest and buffalo abundance in both the wet and dry seasons. More solitary females occurred in areas of low buffalo abundance where wildebeest were in medium to high abundance and more groups of females occurred in areas of medium buffalo abundance and high wildebeest abundance (Chapter Five).
16. Cub group size in the wet season was not affected by the biotic and abiotic factors investigated. However, in the dry season, cub group size was affected by wildebeest abundance. More large cub groups (five and above) occurred in areas of lower than higher wildebeest abundance, while for both groups of one to two and three to four cubs, there were more observations in the high than in the low wildebeest abundance areas (Chapter Five).

These results highlight the importance of a number of variables that affect lion spatial socio-ecology, such as buffalo and the variation in rainfall.

Buffalo

Generally, there were larger groups of adults and more sightings than expected in the open tree savanna, which is a habitat favoured by buffalo (Funston *et al.* 1998). I found buffalo to be important to both males and females. Previous studies have highlighted the importance of buffalo to male lions (Packer 1986; Funston *et al.* 1998). Adult female group size may also increase with increased buffalo abundance, as the large buffalo would be more successfully hunted by groups of females (Packer *et al.* 1990; Stander 1992b). The presence of buffalo would also facilitate larger group formation as the carcass provides more meat than other prey (giraffe are an exception).

Rainfall variation

Lion group dynamics varied between rainfall variability regions. The lions exhibited risk-prone behaviour across variability regions, forming larger groups in more variable environments. Resource availability fluctuates to a greater extent in a variable environment therefore it is more advantageous for lions to form larger groups to fulfil their minimum daily food requirements. Larger groups have greater hunting success rates (Schaller 1972; Van Orsdol 1984; Packer & Ruttan 1988) and are also able to capture larger prey (Kruuk 1972; Schaller 1972). The lions in KNP may be exhibiting risk-prone behaviour across regions and in years of extremely high rainfall, to ensure that they meet their minimum daily requirements.

Other factors

As found in previous studies. this study also showed the importance of wildebeest and impala to female lions and impala to male lions (Rudnai 1974; Scheel 1993; Funston *et al.* 1998).

Cub group sizes peaked in the woodlands. Although nutrition is a vital element in cub survival (Packer & Pusey 1995) there are other factors such as infanticide (Pusey & Packer 1994) that affect cub survival and hence cub and subadult group size. Woodlands may be important habitats as they provide shelter for cubs from infanticidal males.

The interaction effects of the various processes and patterns were also found to be important in the determination of group size distributions. This highlights the fact that it is the combination of factors that affect spatial socio-ecology of animals. While mechanisms that look at individual levels are important for discerning those elements that are important, it is crucial to look at the interactions between these levels to determine their relative importance in influencing the

dynamics of a population. It is only in this way that we can begin to understand how the system works and how it should be managed for optimality.

Long-term studies are vital for discerning the complex patterns in ecological systems (Franklin 1989). While funding and time budgets generally limit projects to short-term studies, a continuous monitoring system can provide data for short-term projects and allow for the study of long-term effects. The monitoring system of carnivores in KNP, while providing information for short-term management decisions has proved a valuable resource for looking at broad-scale patterns across a large, heterogeneous environment. There are biases involved when working with long-term data of this nature and therefore caution should be exercised when extrapolating from the results. However, my results have shown that one can obtain sensible results from analysis of such data.

The results of my study indicate that habitat structure, environmental variability and the presence of certain key prey species are important to lion spatial socio-ecology. To ensure the successful continuation of this lion population, without compromising other predators and prey species, it is vital that the heterogeneity of the park is maintained. A heterogeneous environment comprises areas of different prey availability, habitat structures and habitat quality/ variability (Du Toit 1995), while a homogenous environment would have one habitat type of consistent structure and quality with the same prey composition throughout. Species diversity is greater where there is more habitat variety (Rosenzweig 1995). A heterogeneous environment would ensure that one predator species was not dominant throughout the area. Different habitats result in different prey compositions as herbivores differ in their habitat preferences (Du Toit 1995), which would in turn affect predator distribution and density. Changing conditions of an area that inadvertently result in ideal habitats for certain predators such as the lion, could lead to the rapid decline of other predators. The decline of prey species not normally favoured by that predator may also occur because an area that was previously unfavourable becomes favourable (Mills 1991). An example of this occurred in KNP when waterholes were opened in the north (Harrington *et al.* 1999). The influx of wildebeest and zebra into the area resulted in an increase in lions, which then also preyed on the roan antelope (Harrington *et al.* 1999). It is more important to maintain an environment that can support both common and rare species, than an environment where one species survives to the detriment of others. In order to successfully conserve the diversity of animals in any reserve it is vital to maintain the heterogeneity of habitats within that environment that is required to support them.

Currently in KNP, a new elephant management plan has been proposed that focuses on the extent and intensity of elephant impacts on biodiversity, rather than on elephant numbers, as was the case in the past (Cumming 1982; Van Aarde, Whyte & Pimm 1999; Whyte, Biggs, Gaylard & Braack 1999). Elephants have a major impact on vegetation, resulting in a change from savanna woodlands to wooded grasslands or even grasslands (Buechner & Dawkins 1961; Eltringham 1980; Tchamba & Mahamat 1992). While this has a negative impact on biodiversity, the total exclusion of elephants can also negatively impact on biodiversity (Whyte *et al.* 1999). The new management policy proposes to divide KNP into six zones, namely two botanical reserves, two high-elephant-impact zones and two low-elephant-impact zones (Whyte *et al.* 1999). Elephant numbers will not be reduced in the high-elephant-impact zones, while numbers will be actively reduced in the low-elephant-impact zones (Whyte *et al.* 1999). It is hoped that the impact zones may be alternated so as to prevent the irreversible reduction of biodiversity in the areas of high impact (Whyte *et al.* 1999).

According to Whyte *et al.* (1999) the low-elephant-impact zone to be established in the central district of KNP may in fact be zoned as a high impact zone. This is a key lion area. As stated above, elephants have a tremendous effect on woodlands, often reducing them to grasslands. While this study and others have shown lions to select open tree savanna, they also show a preference for thickets (Mills & Biggs 1993; Mills & Gorman 1997). The change in habitat structure will therefore impact on lion distribution. While the zones of high and low impact may be alternated in time, the effects of elephant utilisation on the vegetation may not be reversed. Therefore while the aim of managing elephant impact on the environment is to ensure maximum biodiversity, there are other consequences that should be taken into consideration.

In terms of ensuring the conservation of small lion populations, my study has highlighted the importance of habitat structure, certain prey species and rainfall variability in determining lion group dynamics. Although my results indicate general patterns of lion biology and results can be extrapolated from this study to other populations or areas, caution should be exercised as biological systems are dynamic and will not be identical (Mills 1991). As found in this study and others (e.g. Mills & Biggs 1993; Mills & Gorman 1997), open tree savanna and thickets are important to lions. This emphasises the need for heterogeneous environments, as the two habitats confer different advantages to lions. While the open tree savanna supports favoured lion prey species such as buffalo, zebra and wildebeest, thickets provide protected areas for cubs.

Rainfall variability also affects lions through its influence on the environment and hence prey availability. In very variable environments it is better to form larger groups in order to fulfil daily minimum requirements. If the prey base does not contain large prey such as buffalo, larger lion groups cannot be sustained, or if lion prides are small, forming larger groups may not be possible and therefore these lions may suffer. Although solitary individuals are also able to fulfil their daily minimum requirements in variable environments, solitary lions are more susceptible to inter- and intra-specific competition.

In terms of prey availability and kills, in my study, buffalo, impala, wildebeest and zebra were found to be important prey species that also influenced lion group dynamics. Although lions are opportunistic hunters (Schaller 1972; Packer *et al.* 1990), they still show preference for certain species and age classes (Scheel 1993). It would therefore be important to ensure these species are maintained at sustainable levels.

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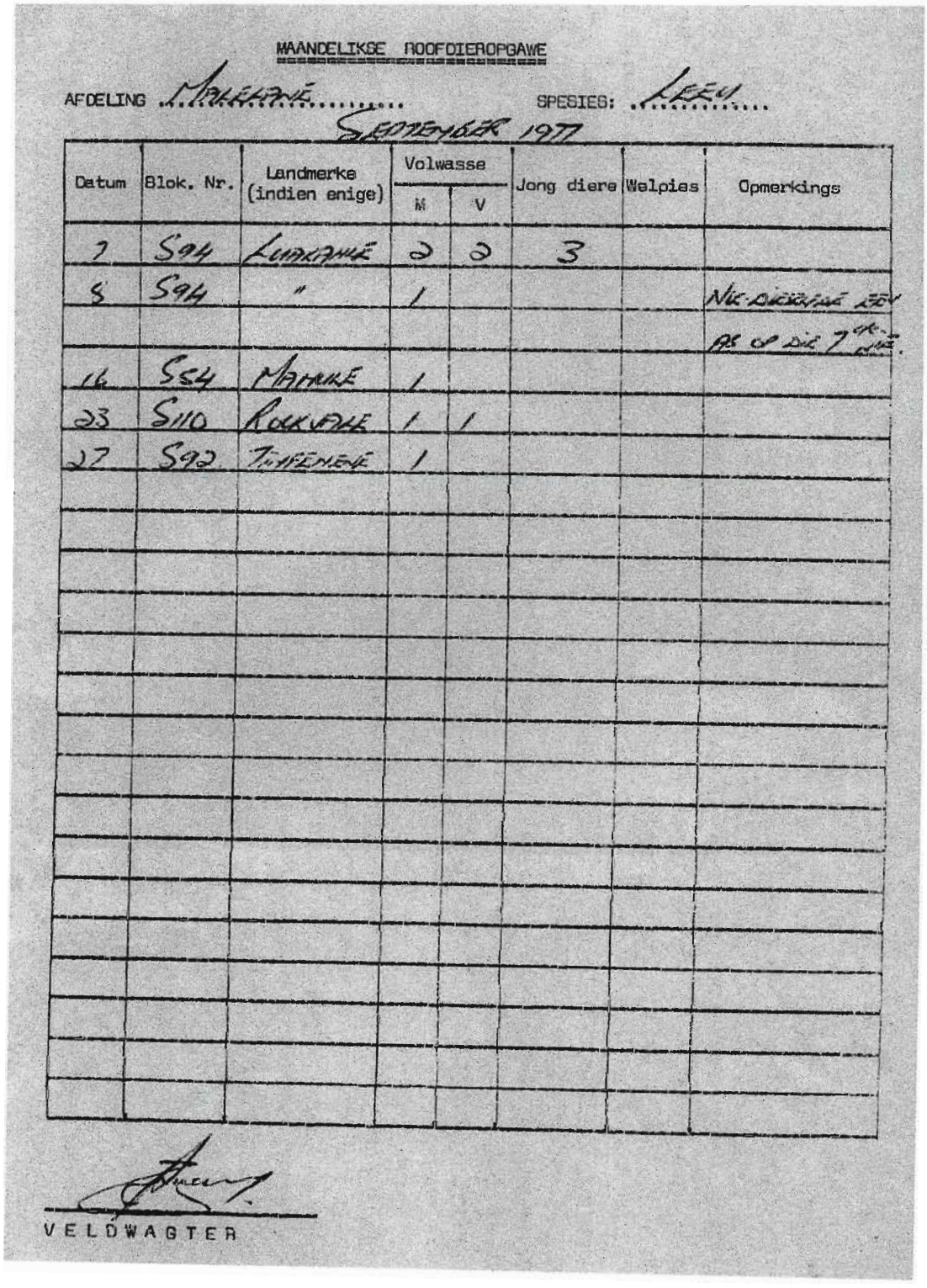
APPENDIX 1.1

Monthly predator return

The following is an example of a monthly predator return from the Malelane ranger station for September 1977. The columns detail the date, block number, location, the number of adults (male and female), subadults/ young lions, cubs and comments.



MAANDELIKSE ROOFDIEROPGAWE

AFDELING Malelane SPESIES: Leeu

September 1977

Datum	Blok. Nr.	Landmerke (indien enige)	Volwasse M	Volwasse V	Jong diere	Welpies	Opmerkings
7	S94	Lumkhane	2	2	3		
8	S94	"	1				Nie diere see as of die 7de.
16	S64	Matjulu	1				
23	S110	Rockdale	1	1			
27	S92	Tamboti	1				

VELDWAGTER

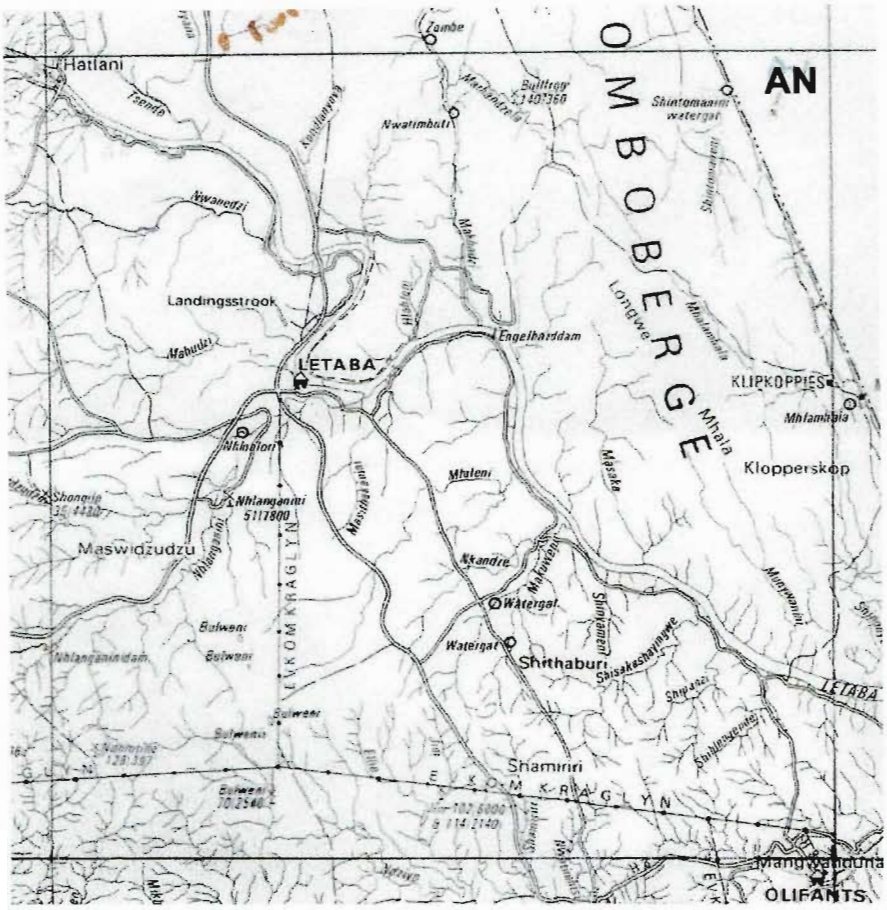
APPENDIX 1.2

Determining grid cell locations

Two 1:250 000 maps of the KNP were obtained from the Technical Services division of the KNP, one detailing the northern and the second detailing the southern sections of the park. The maps are divided into 15min by 15min blocks. I labelled these blocks alphabetically (A-Z, AA-AZ, BA-BZ and CA-CF) beginning in the first north west corner block labelling across the line to the east and repeating this for each row. I made a 225 min^2-grid transparency showing minute squared cells, each corresponding to a number from one to 225, that could be overlaid on each of the 15min by 15min blocks (Fig.1.2.1). By placing the transparency on a block, an underlying location could be assigned a block reference, for example the grid location of Letaba rest camp is AN95 (Fig.1.2.1). This reference system on the hard copy 1:250 000 map corresponded to the cell numbers of the index raster image, Indexhab; e.g. cell one of Indexhab was equal to block reference A1.

This table listing the block reference and corresponding index cell was linked to the table which listed the index cells with their corresponding habitat types. Both tables were imported into an Access database and linked in a relationship joining the index cell column in the block reference table to the index cell column in the habitat table. A query was run which allowed both tables to be displayed. this table was exported as an excel spreadsheet which in turn was imported into a new database.

A list of common location names from each station was made and this was used for determining the grid references. The grid reference (e.g. AB220) for each sighting for which a location could be found on the 1:250 000 maps was recorded on this spreadsheet. This was manually cross-checked with the complete data set and a block reference assigned to all sightings for which a reference could be determined.



Row 1 = cells 1-15
Row 2= cells 16-30
Row 3 = cells 31-45
Row 4 = cells 46-60
Row 5 = cells 61-75
Row 6 = cells 76-90
Row 7 = cells 91-105
Row 8 = cells 106-120
Row 9 = cells 121-135
Row 10 = cells 136-150
Row 11 = cells 151-165
Row 12 = cells 166-180
Row 13 = cells 181-195
Row 14 = cells 196-210
Row 15 = cells 211-225

Figure 1.2.1. A 225 min^2-grid transparency consisting of 225 1-min^2cells was placed over the 225 min^2 grids on a 1:250 000 map of KNP in order to determine the block reference locations of the lion observations recorded in the ranger diaries and on the monthly predator returns. These block references corresponded to the grid cell references of an index raster image.

APPENDIX 1.3

Creation of index map

The cells of an index map are numbered consecutively starting at one and numbered from left to right along the rows. The index map provides a reference system that can be used to link maps of the same dimensions. If one wants to extract specific data from certain cells on an information map, those cell numbers are listed in a database. The index map is used as a reference map to determine from which cells on the information map data needs to be extracted.

The index map, Indexhab, was created in IDRISI by executing the initial function, which copies the parameters from another map (new_map3) to a blank image. As each cell had a zero value and would therefore not appear as a vector file, the zeros were reclassified to have a value of one. This raster image was made into a point vector file using the pointvec function in IDRISI and the vector file imported into Cartalinx. In Cartalinx every file has three associated tables/ databases in which the details of the nodes (point data), arcs (line data) and polygons are listed. The vector file was saved in Cartalinx format. Cartalinx assigned a numerical identifier of one to every point. To change these data, the Cartalinx node database was opened in Microsoft Access and the column contents of NumericalUserID were changed from values of one to values of one through 15444. The file was saved and the Cartalinx vector file was reopened in Cartalinx, the changes made in Access thereby taking effect, i.e. the points had labels numbering one to 15444. The file was then exported as an IDRISI vector file. A blank raster image (Indexhab), created using the initial function, was updated with the vector data using the pointras function in IDRISI. This image has 15444 cells each with an individual identifier.

APPENDIX 1.4

1.4A *Creation of the male to female ratio maps*

The maximum number of females was determined for each three-month period by overlaying the two maximum female images to produce a map of the overall maximum number of females in each cell. The same was done for the adult males. The following macro was executed to determine the adult sex ratio:

```
overlay x 9 jm57mfm jm57mfo jm57mf
overlay x 9 jm58mfm jm58mfo jm58mf
overlay x 9 jm59mfm jm59mfo jm59mf
overlay x 9 jm60mfm jm60mfo jm60mf
overlay x 9 jm61mfm jm61mfo jm61mf
overlay x 9 jm62mfm jm62mfo jm62mf
overlay x 9 jm63mfm jm63mfo jm63mf
overlay x 9 jm64mfm jm64mfo jm64mf
overlay x 9 jm65mfm jm65mfo jm65mf
overlay x 9 jm66mfm jm66mfo jm66mf
overlay x 9 jm67mfm jm67mfo jm67mf
overlay x 9 jm68mfm jm68mfo jm68mf
overlay x 9 jm69mfm jm69mfo jm69mf
overlay x 9 jm70mfm jm70mfo jm70mf
overlay x 9 jm71mfm jm71mfo jm71mf
overlay x 9 jm72mfm jm72mfo jm72mf
overlay x 9 jm73mfm jm73mfo jm73mf
overlay x 9 jm74mfm jm74mfo jm74mf
overlay x 9 jm75mfm jm75mfo jm75mf
overlay x 9 jm76mfm jm76mfo jm76mf
overlay x 9 jm77mfm jm77mfo jm77mf
overlay x 9 jm78mfm jm78mfo jm78mf
overlay x 9 jm79mfm jm79mfo jm79mf
overlay x 9 jm80mfm jm80mfo jm80mf
overlay x 9 jm81mfm jm81mfo jm81mf
overlay x 9 jm82mfm jm82mfo jm82mf
overlay x 9 jm83mfm jm83mfo jm83mf
overlay x 9 jm84mfm jm84mfo jm84mf
overlay x 9 jm85mfm jm85mfo jm85mf
```

Step 1

```
reclass x i jm57mf jm57mfr 3 backgrnd
reclass x i jm58mf jm58mfr 3 backgrnd
reclass x i jm59mf jm59mfr 3 backgrnd
reclass x i jm60mf jm60mfr 3 backgrnd
reclass x i jm61mf jm61mfr 3 backgrnd
reclass x i jm62mf jm62mfr 3 backgrnd
reclass x i jm63mf jm63mfr 3 backgrnd
reclass x i jm64mf jm64mfr 3 backgrnd
reclass x i jm65mf jm65mfr 3 backgrnd
reclass x i jm66mf jm66mfr 3 backgrnd
reclass x i jm67mf jm67mfr 3 backgrnd
reclass x i jm68mf jm68mfr 3 backgrnd
reclass x i jm69mf jm69mfr 3 backgrnd
reclass x i jm70mf jm70mfr 3 backgrnd
reclass x i jm71mf jm71mfr 3 backgrnd
reclass x i jm72mf jm72mfr 3 backgrnd
reclass x i jm73mf jm73mfr 3 backgrnd
reclass x i jm74mf jm74mfr 3 backgrnd
reclass x i jm75mf jm75mfr 3 backgrnd
reclass x i jm76mf jm76mfr 3 backgrnd
reclass x i jm77mf jm77mfr 3 backgrnd
reclass x i jm78mf jm78mfr 3 backgrnd
reclass x i jm79mf jm79mfr 3 backgrnd
reclass x i jm80mf jm80mfr 3 backgrnd
reclass x i jm81mf jm81mfr 3 backgrnd
reclass x i jm82mf jm82mfr 3 backgrnd
reclass x i jm83mf jm83mfr 3 backgrnd
reclass x i jm84mf jm84mfr 3 backgrnd
reclass x i jm85mf jm85mfr 3 backgrnd
```

Step 2

```
overlay x 9 jm57mmm jm57mmo jm57mm
overlay x 9 jm58mmm jm58mmo jm58mm
overlay x 9 jm59mmm jm59mmo jm59mm
overlay x 9 jm60mmm jm60mmo jm60mm
overlay x 9 jm61mmm jm61mmo jm61mm
overlay x 9 jm62mmm jm62mmo jm62mm
overlay x 9 jm63mmm jm63mmo jm63mm
overlay x 9 jm64mmm jm64mmo jm64mm
overlay x 9 jm65mmm jm65mmo jm65mm
overlay x 9 jm66mmm jm66mmo jm66mm
overlay x 9 jm67mmm jm67mmo jm67mm
overlay x 9 jm68mmm jm68mmo jm68mm
overlay x 9 jm69mmm jm69mmo jm69mm
overlay x 9 jm70mmm jm70mmo jm70mm
overlay x 9 jm71mmm jm71mmo jm71mm
overlay x 9 jm72mmm jm72mmo jm72mm
overlay x 9 jm73mmm jm73mmo jm73mm
overlay x 9 jm74mmm jm74mmo jm74mm
overlay x 9 jm75mmm jm75mmo jm75mm
overlay x 9 jm76mmm jm76mmo jm76mm
overlay x 9 jm77mmm jm77mmo jm77mm
overlay x 9 jm78mmm jm78mmo jm78mm
overlay x 9 jm79mmm jm79mmo jm79mm
overlay x 9 jm80mmm jm80mmo jm80mm
overlay x 9 jm81mmm jm81mmo jm81mm
overlay x 9 jm82mmm jm82mmo jm82mm
overlay x 9 jm83mmm jm83mmo jm83mm
overlay x 9 jm84mmm jm84mmo jm84mm
overlay x 9 jm85mmm jm85mmo jm85mm
overlay x 4 jm57mm jm57mfr jm57mmfm
overlay x 4 jm58mm jm58mfr jm58mmfm
overlay x 4 jm59mm jm59mfr jm59mmfm
overlay x 4 jm60mm jm60mfr jm60mmfm
overlay x 4 jm61mm jm61mfr jm61mmfm
overlay x 4 jm62mm jm62mfr jm62mmfm
overlay x 4 jm63mm jm63mfr jm63mmfm
overlay x 4 jm64mm jm64mfr jm64mmfm
overlay x 4 jm65mm jm65mfr jm65mmfm
overlay x 4 jm66mm jm66mfr jm66mmfm
overlay x 4 jm67mm jm67mfr jm67mmfm
overlay x 4 jm68mm jm68mfr jm68mmfm
overlay x 4 jm69mm jm69mfr jm69mmfm
overlay x 4 jm70mm jm70mfr jm70mmfm
overlay x 4 jm71mm jm71mfr jm71mmfm
overlay x 4 jm72mm jm72mfr jm72mmfm
overlay x 4 jm73mm jm73mfr jm73mmfm
overlay x 4 jm74mm jm74mfr jm74mmfm
overlay x 4 jm75mm jm75mfr jm75mmfm
overlay x 4 jm76mm jm76mfr jm76mmfm
overlay x 4 jm77mm jm77mfr jm77mmfm
overlay x 4 jm78mm jm78mfr jm78mmfm
overlay x 4 jm79mm jm79mfr jm79mmfm
overlay x 4 jm80mm jm80mfr jm80mmfm
overlay x 4 jm81mm jm81mfr jm81mmfm
overlay x 4 jm82mm jm82mfr jm82mmfm
overlay x 4 jm83mm jm83mfr jm83mmfm
overlay x 4 jm84mm jm84mfr jm84mmfm
overlay x 4 jm85mm jm85mfr jm85mmfm
reclass X i jm57mmfm jm57mmfR 3 tester
reclass X i jm58mmfm jm58mmfR 3 tester
reclass X i jm59mmfm jm59mmfR 3 tester
reclass X i jm60mmfm jm60mmfR 3 tester
reclass X i jm61mmfm jm61mmfR 3 tester
reclass X i jm62mmfm jm62mmfR 3 tester
reclass X i jm63mmfm jm63mmfR 3 tester
reclass X i jm64mmfm jm64mmfR 3 tester
reclass X i jm65mmfm jm65mmfR 3 tester
reclass X i jm66mmfm jm66mmfR 3 tester
reclass X i jm67mmfm jm67mmfR 3 tester
reclass X i jm68mmfm jm68mmfR 3 tester
reclass X i jm69mmfm jm69mmfR 3 tester
reclass X i jm70mmfm jm70mmfR 3 tester
reclass X i jm71mmfm jm71mmfR 3 tester
```

Step 3

Step 4

Step 5

```
reclass X i jm72mmfm jm72mmfR 3 tester
reclass X i jm73mmfm jm73mmfR 3 tester
reclass X i jm74mmfm jm74mmfR 3 tester
reclass X i jm75mmfm jm75mmfR 3 tester
reclass X i jm76mmfm jm76mmfR 3 tester
reclass X i jm77mmfm jm77mmfR 3 tester
reclass X i jm78mmfm jm78mmfR 3 tester
reclass X i jm79mmfm jm79mmfR 3 tester
reclass X i jm80mmfm jm80mmfR 3 tester
reclass X i jm81mmfm jm81mmfR 3 tester
reclass X i jm82mmfm jm82mmfR 3 tester
reclass X i jm83mmfm jm83mmfR 3 tester
reclass X i jm84mmfm jm84mmfR 3 tester
reclass X i jm85mmfm jm85mmfR 3 tester
```

Step 5

```
overlay X 1 jm57mmfR jm58mmfR jmmmfR1
overlay X 1 jmmmfR1 jm59mmfR jmmmfR2
overlay X 1 jmmmfR2 jm60mmfR jmmmfR3
overlay X 1 jmmmfR3 jm61mmfR jmmmfR4
overlay X 1 jmmmfR4 jm62mmfR jmmmfR5
overlay X 1 jmmmfR5 jm63mmfR jmmmfR6
overlay X 1 jmmmfR6 jm64mmfR jmmmfR7
overlay X 1 jmmmfR7 jm65mmfR jmmmfR8
overlay X 1 jmmmfR8 jm66mmfR jmmmfR9
overlay X 1 jmmmfR9 jm67mmfR jmmmfR10
overlay X 1 jmmmfR10 jm68mmfR jmmmfR11
overlay X 1 jmmmfR11 jm69mmfR jmmmfR12
overlay X 1 jmmmfR12 jm70mmfR jmmmfR13
overlay X 1 jmmmfR13 jm71mmfR jmmmfR14
overlay X 1 jmmmfR14 jm72mmfR jmmmfR15
overlay X 1 jmmmfR15 jm73mmfR jmmmfR16
overlay X 1 jmmmfR16 jm74mmfR jmmmfR17
overlay X 1 jmmmfR17 jm75mmfR jmmmfR18
overlay X 1 jmmmfR18 jm76mmfR jmmmfR19
overlay X 1 jmmmfR19 jm77mmfR jmmmfR20
overlay X 1 jmmmfR20 jm78mmfR jmmmfR21
overlay X 1 jmmmfR21 jm79mmfR jmmmfR22
overlay X 1 jmmmfR22 jm80mmfR jmmmfR23
overlay X 1 jmmmfR23 jm81mmfR jmmmfR24
overlay X 1 jmmmfR24 jm82mmfR jmmmfR25
overlay X 1 jmmmfR25 jm83mmfR jmmmfR26
overlay X 1 jmmmfR26 jm84mmfR jmmmfR27
overlay X 1 jmmmfR27 jm85mmfR jmmmfRpF
reclass X i jmmmfRpF jmmmfRF 3 backgrnd
```

Step 6

```
overlay X 1 jm57mmfm jm58mmfm jmmmfm1
overlay X 1 jmmmfm1 jm59mmfm jmmmfm2
overlay X 1 jmmmfm2 jm60mmfm jmmmfm3
overlay X 1 jmmmfm3 jm61mmfm jmmmfm4
overlay X 1 jmmmfm4 jm62mmfm jmmmfm5
overlay X 1 jmmmfm5 jm63mmfm jmmmfm6
overlay X 1 jmmmfm6 jm64mmfm jmmmfm7
overlay X 1 jmmmfm7 jm65mmfm jmmmfm8
overlay X 1 jmmmfm8 jm66mmfm jmmmfm9
overlay X 1 jmmmfm9 jm67mmfm jmmmfm10
overlay X 1 jmmmfm10 jm68mmfm jmmmfm11
overlay X 1 jmmmfm11 jm69mmfm jmmmfm12
overlay X 1 jmmmfm12 jm70mmfm jmmmfm13
overlay X 1 jmmmfm13 jm71mmfm jmmmfm14
overlay X 1 jmmmfm14 jm72mmfm jmmmfm15
overlay X 1 jmmmfm15 jm73mmfm jmmmfm16
overlay X 1 jmmmfm16 jm74mmfm jmmmfm17
overlay X 1 jmmmfm17 jm75mmfm jmmmfm18
overlay X 1 jmmmfm18 jm76mmfm jmmmfm19
overlay X 1 jmmmfm19 jm77mmfm jmmmfm20
overlay X 1 jmmmfm20 jm78mmfm jmmmfm21
overlay X 1 jmmmfm21 jm79mmfm jmmmfm22
overlay X 1 jmmmfm22 jm80mmfm jmmmfm23
overlay X 1 jmmmfm23 jm81mmfm jmmmfm24
overlay X 1 jmmmfm24 jm82mmfm jmmmfm25
overlay X 1 jmmmfm25 jm83mmfm jmmmfm26
overlay X 1 jmmmfm26 jm84mmfm jmmmfm27
overlay X 1 jmmmfm27 jm85mmfm jmmmfmF
overlay X 4 jmmmfmF jmmmfRF jmmmfin
```

Step 7

In step one, the absolute maximum number of adult females was calculated for each year of the period. As the map of the number of males was divided by the map of the number of females, the female maps for each period had to be reclassified so that the background cells were given a value of −1 (Step two). The absolute maximum number of adult males in each year was determined in step three. In Step four the maximum adult male maps created in step three were divided by the corresponding maximum adult female maps created in step two. These maps were reclassified to create the final map for division in step seven (Step five). The maps for each period were summed (step six), the final products of which were added and divided by the number of records in each cell (final map of step five) to get an average for the 29-year period. Unfortunately, ratios of males to females were only obtained where both males and females had been recorded in the cell. Where only females had been sighted, the resulting cell in the final map would have a zero value and where only males had been recorded the cell would reflect a negative number (value divided by −1).

1.4B *Creation of cub to female ratios maps*

The map of maximum cubs recorded was divided by the reclassified map of maximum females, as determined in the male to female ratio macro, to obtain a map of the cub to female ratio for each three-month period. These were averaged over the 28-year period. The following example shows the structure of the macro used, this macro relates to the Oct-Dec period data. In step one, the maps of maximum cub group size were overlaid by the corresponding reclassified maximum adult female maps as created in step two of the adult sex ratio macro (Appendix 1.4A). In step two, the ratio maps of each year were reclassified for the final division. The reclassified maps were added (step three) as were the ratio maps (step four), the final product of each step was overlaid to create the final averaged cub to female ratio map.

```
overlay x 4 od57mcub od57mfr od57cbfm
overlay x 4 od58mcub od58mfr od58cbfm
overlay x 4 od59mcub od59mfr od59cbfm
overlay x 4 od60mcub od60mfr od60cbfm
overlay x 4 od61mcub od61mfr od61cbfm
overlay x 4 od62mcub od62mfr od62cbfm
overlay x 4 od63mcub od63mfr od63cbfm
overlay x 4 od64mcub od64mfr od64cbfm
overlay x 4 od65mcub od65mfr od65cbfm
overlay x 4 od66mcub od66mfr od66cbfm
overlay x 4 od67mcub od67mfr od67cbfm
overlay x 4 od68mcub od68mfr od68cbfm
overlay x 4 od69mcub od69mfr od69cbfm
overlay x 4 od70mcub od70mfr od70cbfm
overlay x 4 od71mcub od71mfr od71cbfm
overlay x 4 od72mcub od72mfr od72cbfm
overlay x 4 od73mcub od73mfr od73cbfm
overlay x 4 od74mcub od74mfr od74cbfm
overlay x 4 od75mcub od75mfr od75cbfm
overlay x 4 od76mcub od76mfr od76cbfm
overlay x 4 od77mcub od77mfr od77cbfm
overlay x 4 od78mcub od78mfr od78cbfm
overlay x 4 od79mcub od79mfr od79cbfm
overlay x 4 od80mcub od80mfr od80cbfm
overlay x 4 od81mcub od81mfr od81cbfm
overlay x 4 od82mcub od82mfr od82cbfm
overlay x 4 od83mcub od83mfr od83cbfm
overlay x 4 od84mcub od84mfr od84cbfm
overlay x 4 od85mcub od85mfr od85cbfm
```

Step 1

```
reclass X i od57cbfm od57cfR 3 tester
reclass X i od58cbfm od58cfR 3 tester
reclass X i od59cbfm od59cfR 3 tester
reclass X i od60cbfm od60cfR 3 tester
reclass X i od61cbfm od61cfR 3 tester
reclass X i od62cbfm od62cfR 3 tester
reclass X i od63cbfm od63cfR 3 tester
reclass X i od64cbfm od64cfR 3 tester
reclass X i od65cbfm od65cfR 3 tester
reclass X i od66cbfm od66cfR 3 tester
reclass X i od67cbfm od67cfR 3 tester
reclass X i od68cbfm od68cfR 3 tester
reclass X i od69cbfm od69cfR 3 tester
reclass X i od70cbfm od70cfR 3 tester
reclass X i od71cbfm od71cfR 3 tester
reclass X i od72cbfm od72cfR 3 tester
reclass X i od73cbfm od73cfR 3 tester
reclass X i od74cbfm od74cfR 3 tester
reclass X i od75cbfm od75cfR 3 tester
reclass X i od76cbfm od76cfR 3 tester
reclass X i od77cbfm od77cfR 3 tester
```

Step 2

```
reclass X i od78cbfm od78cfR 3 tester
reclass X i od79cbfm od79cfR 3 tester
reclass X i od80cbfm od80cfR 3 tester
reclass X i od81cbfm od81cfR 3 tester
reclass X i od82cbfm od82cfR 3 tester
reclass X i od83cbfm od83cfR 3 tester
reclass X i od84cbfm od84cfR 3 tester
reclass X i od85cbfm od85cfR 3 tester
```

Step 2

```
overlay X 1 od57cfR od58cfR odcfR1
overlay X 1 odcfR1 od59cfR odcfR2
overlay X 1 odcfR2 od60cfR odcfR3
overlay X 1 odcfR3 od61cfR odcfR4
overlay X 1 odcfR4 od62cfR odcfR5
overlay X 1 odcfR5 od63cfR odcfR6
overlay X 1 odcfR6 od64cfR odcfR7
overlay X 1 odcfR7 od65cfR odcfR8
overlay X 1 odcfR8 od66cfR odcfR9
overlay X 1 odcfR9 od67cfR odcfR10
overlay X 1 odcfR10 od68cfR odcfR11
overlay X 1 odcfR11 od69cfR odcfR12
overlay X 1 odcfR12 od70cfR odcfR13
overlay X 1 odcfR13 od71cfR odcfR14
overlay X 1 odcfR14 od72cfR odcfR15
overlay X 1 odcfR15 od73cfR odcfR16
overlay X 1 odcfR16 od74cfR odcfR17
overlay X 1 odcfR17 od75cfR odcfR18
overlay X 1 odcfR18 od76cfR odcfR19
overlay X 1 odcfR19 od77cfR odcfR20
overlay X 1 odcfR20 od78cfR odcfR21
overlay X 1 odcfR21 od79cfR odcfR22
overlay X 1 odcfR22 od80cfR odcfR23
overlay X 1 odcfR23 od81cfR odcfR24
overlay X 1 odcfR24 od82cfR odcfR25
overlay X 1 odcfR25 od83cfR odcfR26
overlay X 1 odcfR26 od84cfR odcfR27
overlay X 1 odcfR27 od85cfR odcfRpF
reclass X i odcfRpF odcfRF 3 backgrnd
```

Step 3

```
overlay X 1 od57cbfm od58cbfm odcbfm1
overlay X 1 odcbfm1 od59cbfm odcbfm2
overlay X 1 odcbfm2 od60cbfm odcbfm3
overlay X 1 odcbfm3 od61cbfm odcbfm4
overlay X 1 odcbfm4 od62cbfm odcbfm5
overlay X 1 odcbfm5 od63cbfm odcbfm6
overlay X 1 odcbfm6 od64cbfm odcbfm7
overlay X 1 odcbfm7 od65cbfm odcbfm8
overlay X 1 odcbfm8 od66cbfm odcbfm9
overlay X 1 odcbfm9 od67cbfm odcbfm10
overlay X 1 odcbfm10 od68cbfm odcbfm11
overlay X 1 odcbfm11 od69cbfm odcbfm12
overlay X 1 odcbfm12 od70cbfm odcbfm13
overlay X 1 odcbfm13 od71cbfm odcbfm14
overlay X 1 odcbfm14 od72cbfm odcbfm15
overlay X 1 odcbfm15 od73cbfm odcbfm16
overlay X 1 odcbfm16 od74cbfm odcbfm17
overlay X 1 odcbfm17 od75cbfm odcbfm18
overlay X 1 odcbfm18 od76cbfm odcbfm19
overlay X 1 odcbfm19 od77cbfm odcbfm20
overlay X 1 odcbfm20 od78cbfm odcbfm21
overlay X 1 odcbfm21 od79cbfm odcbfm22
overlay X 1 odcbfm22 od80cbfm odcbfm23
overlay X 1 odcbfm23 od81cbfm odcbfm24
overlay X 1 odcbfm24 od82cbfm odcbfm25
overlay X 1 odcbfm25 od83cbfm odcbfm26
overlay X 1 odcbfm26 od84cbfm odcbfm27
overlay X 1 odcbfm27 od85cbfm odcbfmF
overlay X 4 odcbfmF odcfRF odmcffin
```

Step 4

APPENDIX 1.5

Creation of the seasonal variable maps

For convenience and to prevent errors, the maximum and minimum and averages and number of sightings were calculated in two spreadsheets for each period, which were later combined into one table in Excel and used to create Access (version 2.0) databases. The table listing the block reference, index cell and habitat values was imported into each database in turn. The tables were joined in a relationship linking the block reference columns in both tables. A query was run to display all columns from both tables. This table was exported as an excel spreadsheet and checked for errors. As the index and habitat maps are raster based, *i.e.* their structure is that of a grid some sightings that were reported to be on the border were assigned to grid cells that according to the index map fell outside the park. In these cases, a new grid cell location that fell on the border was assigned to the entry. In some cases this resulted in their being more than one line of data for a grid cell, the variables of which were then re-calculated. These tables were once again imported into an Access database (version 2.0) and the properties describing each variable checked for errors and corrected (the maximum, minimum and number of sightings were all integers, while the averaged variable data were single real numbers). As IDRISI only works with single real numbers and integers, the databases were brought into IDRISI through a conversion program that converted all the double real numbers into single real numbers. The databases were opened in the database workshop that resulted in a documentation file being created for each database.

The maps of each variable for each period were created and these maps were added and averaged to create single variable maps for each of the four three-month periods. The following is an example of the average exclusively adult males macro calculated for the three-month period from July-September.

```
reclass X i js57amo js57amoR 3 tester
reclass X i js58amo js58amoR 3 tester
reclass X i js59amo js59amoR 3 tester
reclass X i js60amo js60amoR 3 tester
reclass X i js61amo js61amoR 3 tester
reclass X i js62amo js62amoR 3 tester
reclass X i js63amo js63amoR 3 tester
reclass X i js64amo js64amoR 3 tester
reclass X i js65amo js65amoR 3 tester
reclass X i js66amo js66amoR 3 tester
reclass X i js67amo js67amoR 3 tester
reclass X i js68amo js68amoR 3 tester
reclass X i js69amo js69amoR 3 tester
reclass X i js70amo js70amoR 3 tester
reclass X i js71amo js71amoR 3 tester
reclass X i js72amo js72amoR 3 tester
reclass X i js73amo js73amoR 3 tester
reclass X i js74amo js74amoR 3 tester
reclass X i js75amo js75amoR 3 tester
```

Step 1

```
reclass X i js76amo js76amoR 3 tester
reclass X i js77amo js77amoR 3 tester
reclass X i js78amo js78amoR 3 tester
reclass X i js79amo js79amoR 3 tester
reclass X i js80amo js80amoR 3 tester
reclass X i js81amo js81amoR 3 tester
reclass X i js82amo js82amoR 3 tester
reclass X i js83amo js83amoR 3 tester
reclass X i js84amo js84amoR 3 tester
reclass X i js85amo js85amoR 3 tester
```

Step 1

```
overlay X 1 js57amoR js58amoR jsamoR1
overlay X 1 jsamoR1 js59amoR jsamoR2
overlay X 1 jsamoR2 js60amoR jsamoR3
overlay X 1 jsamoR3 js61amoR jsamoR4
overlay X 1 jsamoR4 js62amoR jsamoR5
overlay X 1 jsamoR5 js63amoR jsamoR6
overlay X 1 jsamoR6 js64amoR jsamoR7
overlay X 1 jsamoR7 js65amoR jsamoR8
overlay X 1 jsamoR8 js66amoR jsamoR9
overlay X 1 jsamoR9 js67amoR jsamoR10
overlay X 1 jsamoR10 js68amoR jsamoR11
overlay X 1 jsamoR11 js69amoR jsamoR12
overlay X 1 jsamoR12 js70amoR jsamoR13
overlay X 1 jsamoR13 js71amoR jsamoR14
overlay X 1 jsamoR14 js72amoR jsamoR15
overlay X 1 jsamoR15 js73amoR jsamoR16
overlay X 1 jsamoR16 js74amoR jsamoR17
overlay X 1 jsamoR17 js75amoR jsamoR18
overlay X 1 jsamoR18 js76amoR jsamoR19
overlay X 1 jsamoR19 js77amoR jsamoR20
overlay X 1 jsamoR20 js78amoR jsamoR21
overlay X 1 jsamoR21 js79amoR jsamoR22
overlay X 1 jsamoR22 js80amoR jsamoR23
overlay X 1 jsamoR23 js81amoR jsamoR24
overlay X 1 jsamoR24 js82amoR jsamoR25
overlay X 1 jsamoR25 js83amoR jsamoR26
overlay X 1 jsamoR26 js84amoR jsamoR27
overlay X 1 jsamoR27 js85amoR jsamoRpF
```

Step 2

```
reclass X i jsamoRpF jsamoRF 3 backgrnd
overlay X 1 js57amo js58amo jsamo1
overlay X 1 jsamo1 js59amo jsamo2
overlay X 1 jsamo2 js60amo jsamo3
overlay X 1 jsamo3 js61amo jsamo4
overlay X 1 jsamo4 js62amo jsamo5
overlay X 1 jsamo5 js63amo jsamo6
overlay X 1 jsamo6 js64amo jsamo7
overlay X 1 jsamo7 js65amo jsamo8
overlay X 1 jsamo8 js66amo jsamo9
overlay X 1 jsamo9 js67amo jsamo10
overlay X 1 jsamo10 js68amo jsamo11
overlay X 1 jsamo11 js69amo jsamo12
overlay X 1 jsamo12 js70amo jsamo13
overlay X 1 jsamo13 js71amo jsamo14
overlay X 1 jsamo14 js72amo jsamo15
overlay X 1 jsamo15 js73amo jsamo16
overlay X 1 jsamo16 js74amo jsamo17
overlay X 1 jsamo17 js75amo jsamo18
overlay X 1 jsamo18 js76amo jsamo19
overlay X 1 jsamo19 js77amo jsamo20
overlay X 1 jsamo20 js78amo jsamo21
overlay X 1 jsamo21 js79amo jsamo22
overlay X 1 jsamo22 js80amo jsamo23
overlay X 1 jsamo23 js81amo jsamo24
overlay X 1 jsamo24 js82amo jsamo25
overlay X 1 jsamo25 js83amo jsamo26
overlay X 1 jsamo26 js84amo jsamo27
overlay X 1 jsamo27 js85amo jsamoF
overlay X 4 jsamoF jsamoRF jsamofin
```

Step 3

```
reclass X i js76amo js76amoR 3 tester
reclass X i js77amo js77amoR 3 tester
reclass X i js78amo js78amoR 3 tester
reclass X i js79amo js79amoR 3 tester
reclass X i js80amo js80amoR 3 tester
reclass X i js81amo js81amoR 3 tester
reclass X i js82amo js82amoR 3 tester
reclass X i js83amo js83amoR 3 tester
reclass X i js84amo js84amoR 3 tester
reclass X i js85amo js85amoR 3 tester
```

Step 1

```
overlay X 1 js57amoR js58amoR jsamoR1
overlay X 1 jsamoR1 js59amoR jsamoR2
overlay X 1 jsamoR2 js60amoR jsamoR3
overlay X 1 jsamoR3 js61amoR jsamoR4
overlay X 1 jsamoR4 js62amoR jsamoR5
overlay X 1 jsamoR5 js63amoR jsamoR6
overlay X 1 jsamoR6 js64amoR jsamoR7
overlay X 1 jsamoR7 js65amoR jsamoR8
overlay X 1 jsamoR8 js66amoR jsamoR9
overlay X 1 jsamoR9 js67amoR jsamoR10
overlay X 1 jsamoR10 js68amoR jsamoR11
overlay X 1 jsamoR11 js69amoR jsamoR12
overlay X 1 jsamoR12 js70amoR jsamoR13
overlay X 1 jsamoR13 js71amoR jsamoR14
overlay X 1 jsamoR14 js72amoR jsamoR15
overlay X 1 jsamoR15 js73amoR jsamoR16
overlay X 1 jsamoR16 js74amoR jsamoR17
overlay X 1 jsamoR17 js75amoR jsamoR18
overlay X 1 jsamoR18 js76amoR jsamoR19
overlay X 1 jsamoR19 js77amoR jsamoR20
overlay X 1 jsamoR20 js78amoR jsamoR21
overlay X 1 jsamoR21 js79amoR jsamoR22
overlay X 1 jsamoR22 js80amoR jsamoR23
overlay X 1 jsamoR23 js81amoR jsamoR24
overlay X 1 jsamoR24 js82amoR jsamoR25
overlay X 1 jsamoR25 js83amoR jsamoR26
overlay X 1 jsamoR26 js84amoR jsamoR27
overlay X 1 jsamoR27 js85amoR jsamoRpF
```

Step 2

```
reclass X i jsamoRpF jsamoRF 3 backgrnd
overlay X 1 js57amo  js58amo  jsamo1
overlay X 1 jsamo1 js59amo  jsamo2
overlay X 1 jsamo2 js60amo  jsamo3
overlay X 1 jsamo3 js61amo  jsamo4
overlay X 1 jsamo4 js62amo  jsamo5
overlay X 1 jsamo5 js63amo  jsamo6
overlay X 1 jsamo6 js64amo  jsamo7
overlay X 1 jsamo7 js65amo  jsamo8
overlay X 1 jsamo8 js66amo  jsamo9
overlay X 1 jsamo9 js67amo  jsamo10
overlay X 1 jsamo10 js68amo  jsamo11
overlay X 1 jsamo11 js69amo  jsamo12
overlay X 1 jsamo12 js70amo  jsamo13
overlay X 1 jsamo13 js71amo  jsamo14
overlay X 1 jsamo14 js72amo  jsamo15
overlay X 1 jsamo15 js73amo  jsamo16
overlay X 1 jsamo16 js74amo  jsamo17
overlay X 1 jsamo17 js75amo  jsamo18
overlay X 1 jsamo18 js76amo  jsamo19
overlay X 1 jsamo19 js77amo  jsamo20
overlay X 1 jsamo20 js78amo  jsamo21
overlay X 1 jsamo21 js79amo  jsamo22
overlay X 1 jsamo22 js80amo  jsamo23
overlay X 1 jsamo23 js81amo  jsamo24
overlay X 1 jsamo24 js82amo  jsamo25
overlay X 1 jsamo25 js83amo  jsamo26
overlay X 1 jsamo26 js84amo  jsamo27
overlay X 1 jsamo27 js85amo  jsamoF
overlay X 4 jsamoF jsamoRF jsamofin
```

Step 3

APPENDIX 1.6

Creation of the annual variable maps

For the final analysis all the data from each period was combined to create one variable map for the entire 28-year period. This was also executed using a macro file. The following macro for calculating the maximum males in mixed group final map is an example showing the structure of the macro used.

```
overlay X 1 jmmmmF ajmmmF mmm1
overlay X 1 mmm1 jsmmmF mmm2
overlay X 1 mmm2 odmmmF mmmfin
overlay X 1 jmmmmRpF ajmmmRpF mmmR1
overlay X 1 mmmR1 jsmmmRpF mmmR2
overlay X 1 mmmR2 odmmmRpF mmmRpfn
reclass X i mmmRpfn mmmRfin 3 backgrnd
overlay X 4 mmmfin mmmRfin mmmall
```

The summed variable map of each three-month period was added (overlay function). The summed reclassified maps were added. Please note that the summed reclassified maps used in this function. were those created before the background values were reclassified in the Appendix 1.5. This map was reclassified so that the background cells had values of –1. The final summed variable map was divided by the final reclassified map to determine the averaged data in each cell for the total time period.

APPENDIX 2.1

Creation of the habitat map

To create the habitat map detailing the four structural classifications described in chapter one, a raster map (Landscap) of the 35 landscape types, as defined by Gertenbach (1983), was obtained from Scientific Services. KNP. This map was resampled in IDRISI to decrease the number of rows from 440 to 240 and columns from 330 to 180. As the boundaries of the new map (Landrsmp) remained constant (NW corner: 22°S; 30°E. SE corner: 26°S; 33°E), resampling the map caused an increase in the cell size to one minute squared. The 35 landscape types of the resampled raster image. Landrsmp, were reclassified to produce a map (new_map2) with four habitat types. The final habitat map (new_map3) was created by windowing new_map2 to decrease the number of rows from 240 to 198 and the number of columns from 180 to 78. This was done to remove the excess redundant cells surrounding the park, thereby making the image smaller and more convenient to work with.

Reference:

Gertenbach, W.P.D. 1983. Landscape patterns of the Kruger National Park. *Koedoe*, **26**: 9-121.

APPENDIX 2.2

Habitat and road area calculation

As the roads are not a minute wide, a second habitat map (maparea) was created from new_map3 in which the number of grid cells was increased by four, i.e. the grid cell size was reduced from one minute^2 to 0.25 minute^2. The area in kilometres squared of each habitat type was calculated. The line vector file of the roads of KNP was added to the second habitat map (maparea) by converting the vector file to a raster image (lineras function). This resulted in a map that provided for a 400-metre buffer zone on either side of the road. The areas of the habitats (with the roads included) were recalculated. By subtracting the last area from the first, the area covered by the roads and buffer zone was determined for each habitat.

APPENDIX 2.3

Obtaining data for analysis

The values file lists the cell number and corresponding data value. The values file was opened in excel where the columns from the table of cell number and corresponding habitat type were pasted alongside the extracted data. Cells without variable data were deleted, as only the cells with variable data were required for analysis. I checked that all three variations (maximum, average, number of sightings) for each of the lion variables had the same amount of data (i.e. all had data in the same cells). Corrections were made where errors had been made and the macros repeated.

The spreadsheets created were saved in Lotus worksheet format (extension *.wks) for use in the statistics package, SPSS.

APPENDIX 3.1

Prey population fluctuation graphs

I totalled the census data for each year for each of the seven focus species and plotted line graphs to show the annual fluctuations in population size for each species (Fig. 3.1.1). All seven populations went through fluctuations with all except buffalo showing a gradual increase in population size from 1978 to 1985.

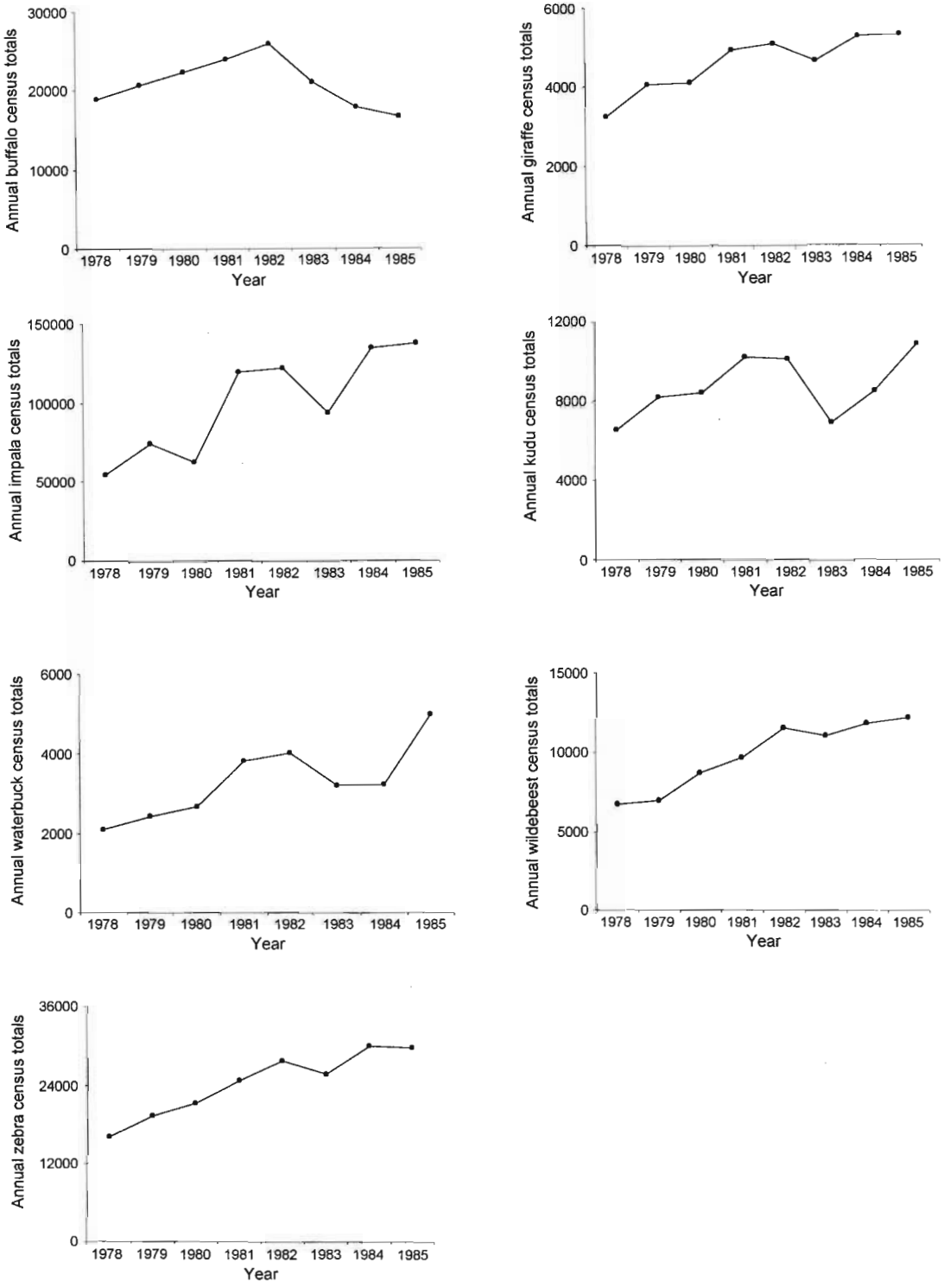


Figure 3.1.1. Annual census totals of seven of the major prey species of lions in KNP over the years 1978 to 1985.

APPENDIX 3.2

Creation of prey maps

I created maps of the same dimensions and cell size as those created for the habitat and lion variable maps. The aerial census data listed the year, species name, longitude, latitude and animal count. To create raster images of these counts for each species for each year I created a tab delimited text file in which the longitude, latitude and animal count were listed. I imported the file into Cartalinx as a point file. The file's associated table contained the following columns: the node identifier, node type (in this case point), numeric user identifier and the three imported columns (longitude, latitude and count). As each point was assigned a numeric user identifier value from 1 to n +1 (the numerical identifier), I replaced these values with the count values, i.e. the point identifiers therefore equaled the count values. I exported this file as an Idrisi point vector file. In order to create raster images of the census data I first created blank images (all cells had a value of zero) using the initial function in Idrisi and copying the parameters from the index map. The blank images are the files that are updated with the vector information in the pointras function when the vector files are converted to raster images. I created raster images for each species for each year.

APPENDIX 3.3

Creation of prey abundance surface maps

I exported the seven Idrisi prey vector files created in Appendix 3.2 as Arcview shape files. I opened the eight files for each species in a separate view in Arcview and ran the surface interpolation function for each vector file to create a surface map for each species for each year. I averaged the surface maps for each species by adding the eight maps together and dividing by eight for each species. I exported the database of the final map in binary raster format. I imported the binary raster image into Idrisi for further analysis.

APPENDIX 3.4

Creation of kill surface maps

I used the data from 1957 to 1988 to create separate kill surface maps for the following species: buffalo, giraffe, impala, kudu, waterbuck, wildebeest and zebra. For each species I created a database of the averaged kills in each cell. I averaged the kills for each species in each cell by the number of years that had that species recorded there, not all years i.e. if four zebra kills were recorded in a cell over a period of three years, average = 4/3 not 4/30. As some areas may have been patrolled more regularly than others, if I had divided by 30, the kills in those areas would be observed more often giving a high kill frequency. Kills in other areas that are patrolled less regularly would be noted less regularly which may result in a low kill frequency being calculated for those areas when this is may not be the case. For example if there were two buffalo kills in one year in cell A and eight kills in eight years in cell B, by averaging for the years when there were kills in each cell, the cells would have values of two and one, respectively. These values better reflect the pattern of kills than if each had divided by 30. Unfortunately, there is bias involved with both methods, as either method could give an accurate measurement of kill frequency across the park depending on whether areas are patrolled equally or infrequently. By dividing by the number of years in which kills were seen, I am generating an index of kill frequency rather than an actual frequency.

I opened each species' database in Idrisi and created raster images for each species using the assign function and the index map (Indexhab). I converted the raster images to point vector files, which I interpolated to create continuous surface maps of kills for each of the seven prey species.

APPENDIX 4.1

Annual rainfall maps

Figures 4.1.1 to 4.1.5 show the annual rainfalls maps created using the following equation:

Rainfall = c + (a * Longitude) − (b * Latitude) + (d * Altitude)

Where a, b and d are the regression coefficients for longitude, latitude and altitude, respectively, and c is the regression constant.

Refer to Chapter Four for details.

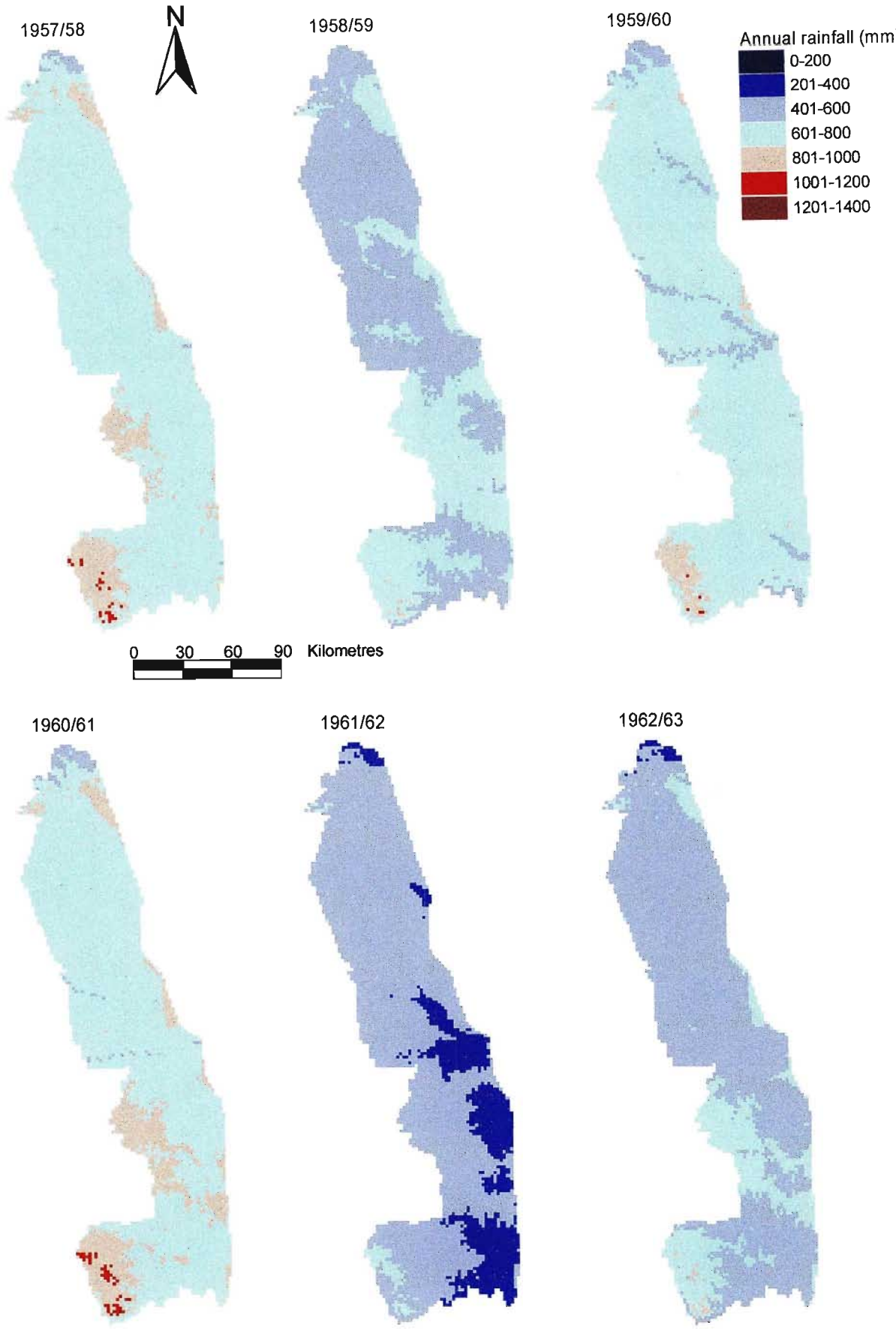


Figure 4.1.1. Annual rainfall maps from 1957/58 to 1962/63. I calculated the annual rainfall from June to July. All the maps have a grid cell size of one minute².

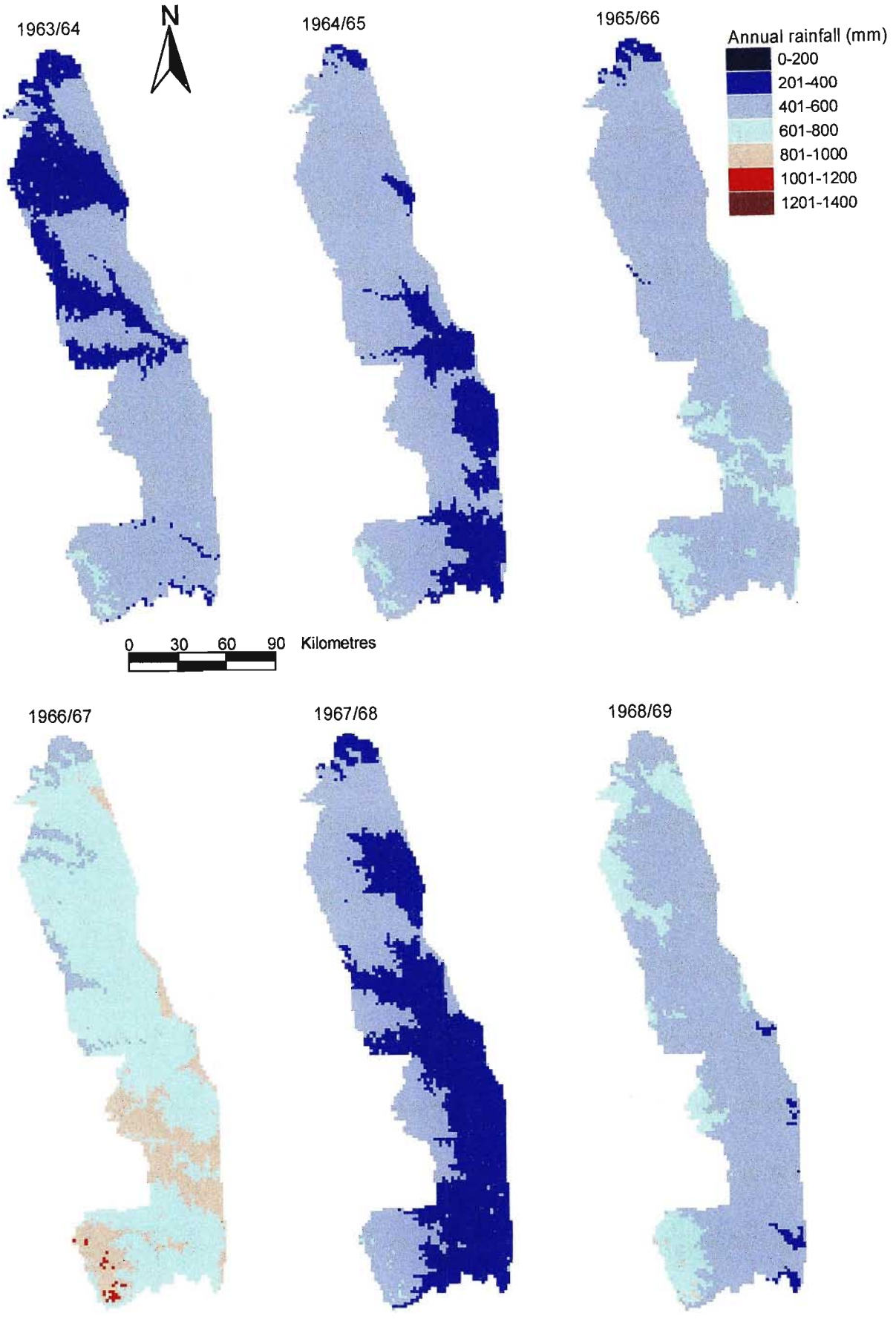


Figure 4.1.2. Annual rainfall maps from 1963/64 to 1968/69. I calculated the annual rainfall from June to July. All the maps have a grid cell size of one minute^2.

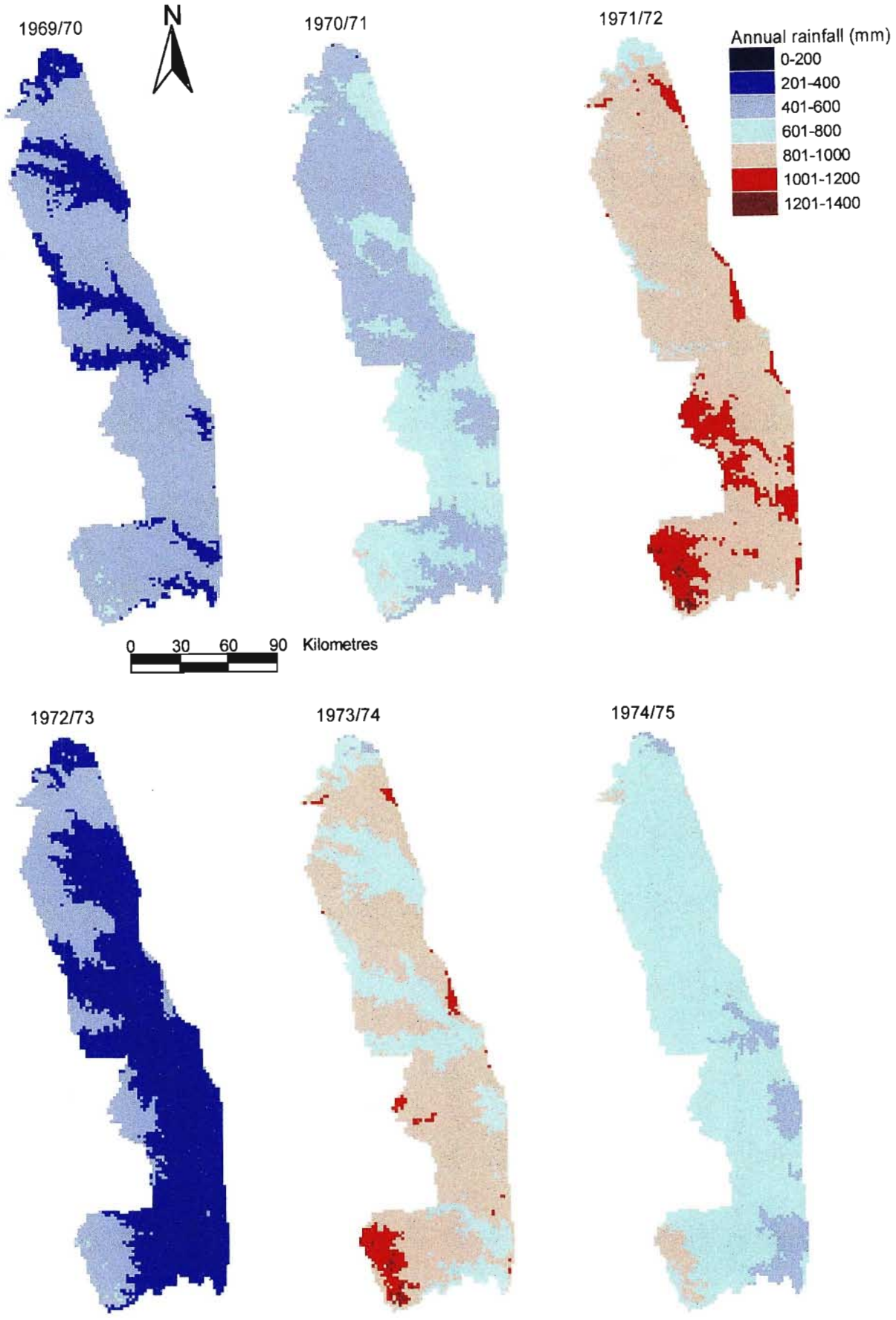


Figure 4.1.3. Annual rainfall maps from 1969/70 to 1974/75. I calculated the annual rainfall from June to July. All the maps have a grid cell size of one minute².

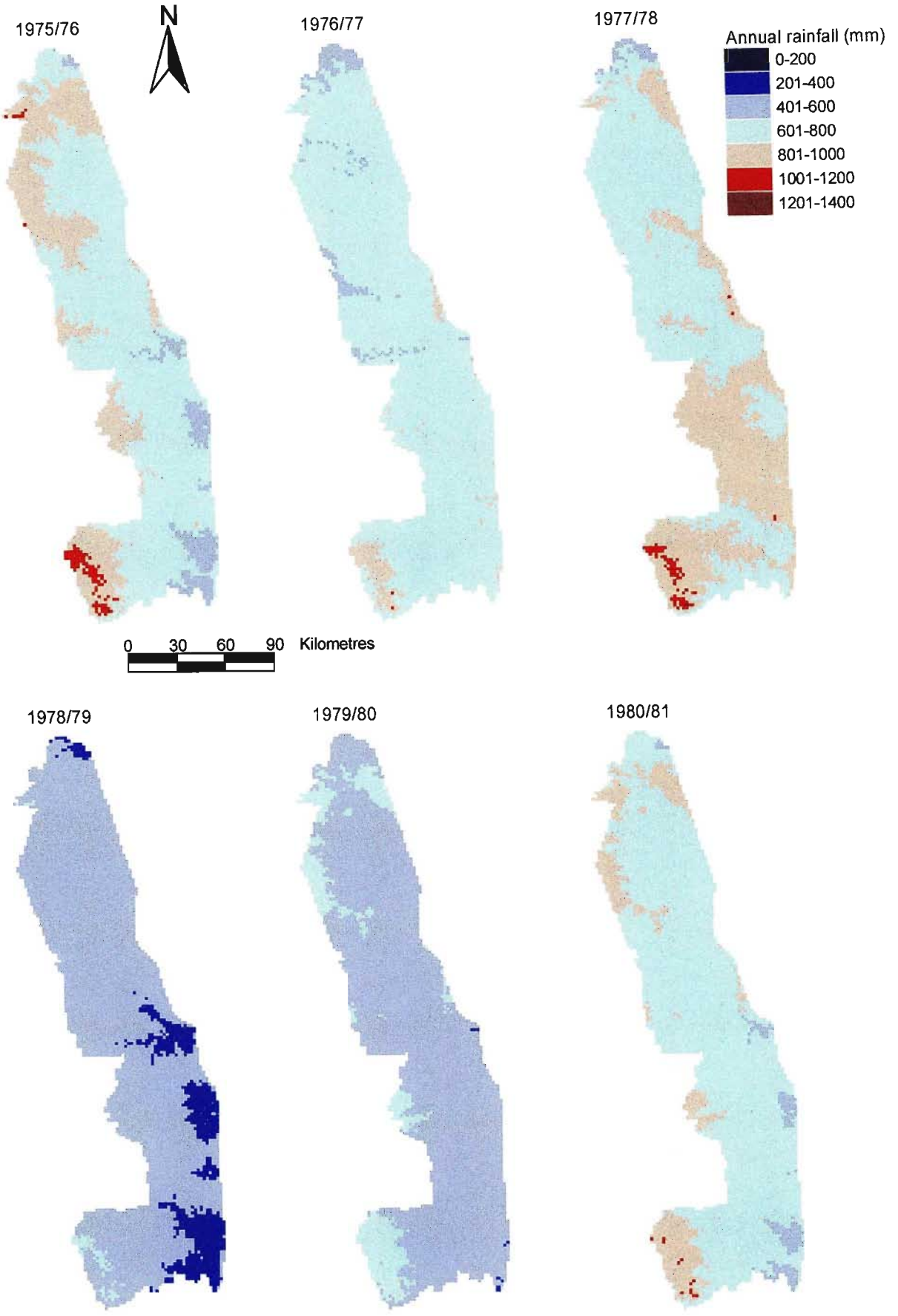


Figure 4.1.4. Annual rainfall maps from 1975/76 to 1980/81. I calculated the annual rainfall from June to July. All the maps have a grid cell size of one minute^2.

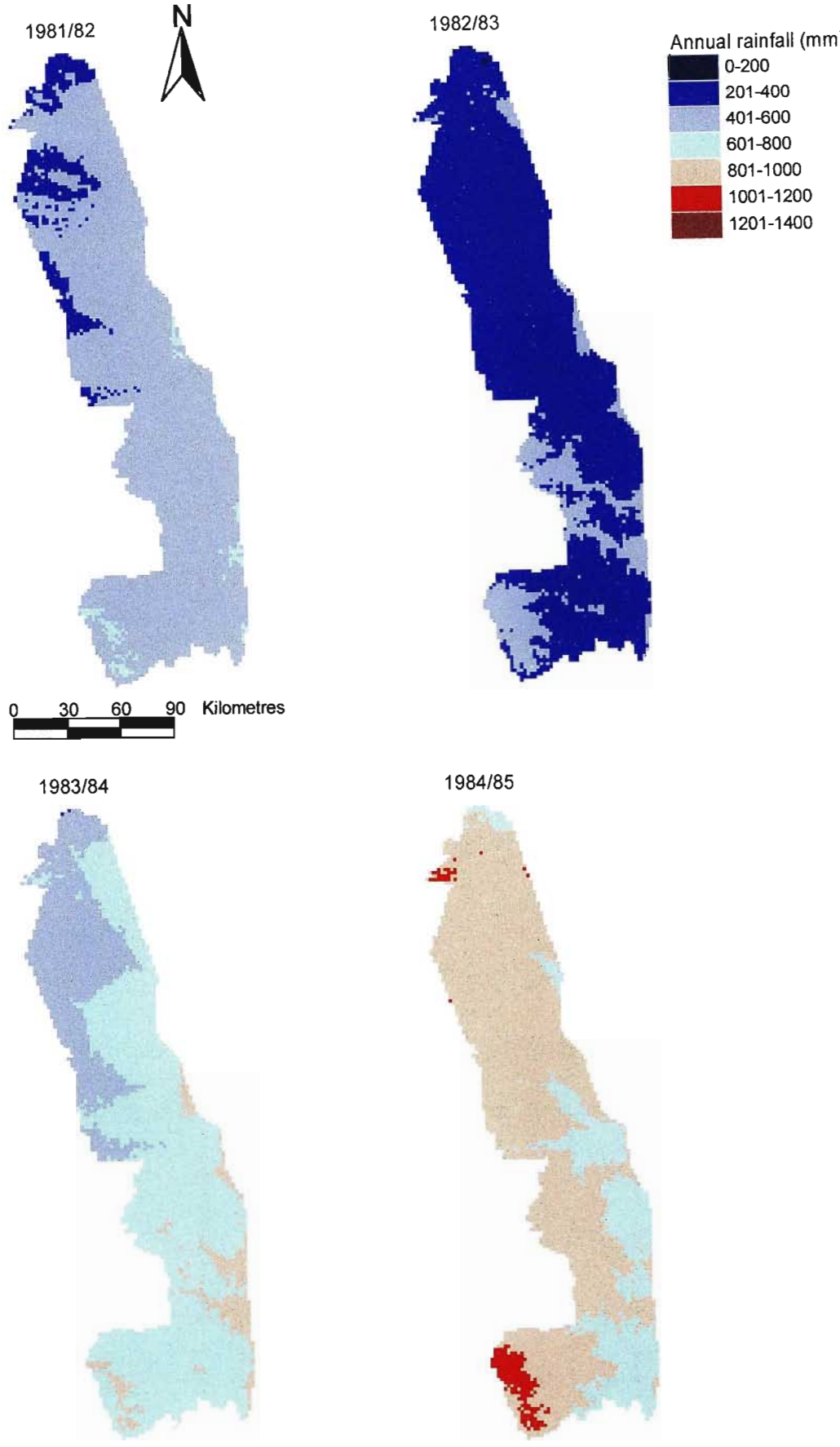


Figure 4.1.5. Annual rainfall maps from 1981/82 to 1984/85. I calculated the annual rainfall from June to July. All the maps have a grid cell size of one minute^2.

APPENDIX X

The folders on the disk contain the information pertaining to Chapters Two to Five as well as the files used in the creation of the index file in Appendix 1.3. Each folder contains a file that details the folders within that folder (Chpt * Folder Explanations). In each folder there is a file that details the files within that folder (Chpt * *** File Explanations; Index Files Explanation).

The raster images and vector files contained in the folders were created in Idrisi 2.0. The databases were created in Microsoft Access version 2.0.

Where data has been presented either in the chapters or in an Appendix (as with the rainfall data). these have not always been included on the cd.